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December 1912

Editor: JOHN M. COULTER

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VOLUME LIV NUMBER 6

THE
BOTANICAL GAZETTE

DECEMBER 1912

THE LIFE HISTORY OF CUTLERIA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 163

SHIGÉO YAMANOUCHI

(WITH FIFTEEN FIGURES AND PLATES XXVI TO XXXV)

Introduction

This paper deals with nuclear conditions in *Cutleria multifida* J. Ag. and *Aglaozonia reptans* Crouan, both of which are found in the Bay of Naples. In common with *Zanardinia*, another member of the Cutleriaceae, *Cutleria* and *Aglaozonia* are characterized by having large motile spores. The vegetative body and method of forming reproductive organs show a combination of characters found in *Ectocarpus*, *Sporochnus*, *Tilopteris*, *Sphacelaria*, *Battersia*, *Zonaria*, *Padina*, and *Laminaria*, genera belonging to different families.

The large motile spores attracted the attention of THURET (**63**), who was the first to do experimental work with *Cutleria multifida*. THURET was followed by many investigators who made cultures of the spores in order to determine whether *Cutleria* and *Aglaozonia* might be two alternating generations of one life cycle, but the results were conflicting.

FALKENBERG (**12**), working with material from Naples, first suggested that *Aglaozonia parvula* is the asexual form of *Cutleria multifida*, and that *Aglaozonia chilosa* is the asexual form of *Cutleria adspersa*. CHURCH (**6**), with material from Plymouth, connected *Aglaozonia reptans* with *Cutleria multifida*, and SAUVAGEAU (**43–51**), with material from Guéthary and Banyuls, proved that

Aglaozonia melanoidea is the asexual form of *Cutleria adspersa*. The conclusions of these authors were drawn chiefly from a comparison of young forms of *Cutleria* collected in nature with young plants obtained from cultures, the emphasis being laid upon outer morphological characters.

It is not necessary to present a detailed historical review of previous work, for many authors, especially SAUVAGEAU (**45**), have given such reviews. Since 1899 no work based upon original investigation has been published except by SAUVAGEAU and the present author. Papers by SAUVAGEAU (**46–51**) confirm his work of 1899, and a paper by the author (**76**) is the preliminary account of the present paper. Before turning to our own investigation, we shall indicate briefly what has been accomplished already, and what still remains to be done.

The first definite account of the discharge and the culture of spores of *Cutleria* was made by THURET (**63**), who observed that the female gametes germinated parthenogenetically. The male plants of *Cutleria* he found to be extremely rare at Saint Vaast-la-Hogue, France, where his cultures were made. This parthenogenetic product, a small plant somewhat resembling *Ectocarpus*, did not live long. According to SAUVAGEAU'S suggestions (**45**) the plant may be designated as form *Thuretiana*. Five years later the brothers CROUAN (**7**), by repeating these observations at Brest, France, came to the same conclusions. DERBÉS and SOLIER (**11**), working on the Mediterranean coast of France, confirmed THURET'S account. Thus these earlier observers, who worked on the French coast, seem to have entertained no doubt of the constancy of the parthenogenetic germination of the female gametes of *Cutleria*.

About two decades later two German botanists, REINKE and FALKENBERG, independently making cultures at the Naples Station, reported quite different results. REINKE (**38, 39**), working at the Station in 1875–1876, observed the actual fertilization of the female gametes by the male gametes of both *Zanardinia* and *Cutleria*. In vessels containing both male and female gametes germination took place freely. There seemed to be no germination of the unfertilized egg. REINKE concluded that sexual reproduction prevailed in *Cutleria multifida* and that THURET must have seen

only exceptional cases of parthenogenesis. He states that in the Bay of Naples the male and female plants occur in the ratio of 3 to 2. He obtained filaments of both *Zanardinia* and *Aglaozonia* which produced non-motile spores. In the cultures of *Cutleria*, *Desmotrichum* finally appeared, and consequently the ultimate products of the fertilized female gametes were not clearly followed.

FALKENBERG (**12**) in 1878, taking great care to obtain pure cultures of both fertilized and unfertilized female gametes, fully demonstrated the necessity of fertilization for germination. The female gametes, entirely separated from the male gametes, retained their capacity for fertilization for four or five days and then never grew beyond the formation of a thin cell membrane. FALKENBERG not only demonstrated the necessity for fertilization, but succeeded in developing the sporelings to a considerable size; in 6–8 weeks the sporeling in the stage of "foot embryo" (*Keimfuss*) had developed as a secondary lateral outgrowth the creeping flat form (*kriechende Flachsprosse*), which is identical with the creeping thallus of *Aglaozonia*. This kind of sporeling may be designated as form *Falkenbergiana*. FALKENBERG was the first to associate *Cutleria multifida* with *Aglaozonia reptans*, and *Cutleria adspersa* with *Aglaozonia chilosa*. Four years later JANCZEWSKI (**21**), at Antibes, did with *Cutleria adspersa* what REINKE and FALKENBERG had done with *Cutleria* at Naples, and showed that unfertilized gametes of *Cutleria adspersa* do not develop further.

In 1894 KUCKUCK (**24**) described a plant under the name of *C. multifida* var. *confervoides*. The plants came up in the tank of the Helgoland Laboratory in the summer of 1893, and were attached to stones which had been collected in the North Haven in fairly shallow water of 1–3 fathoms. The plants were monosiphonic and some of them were in the reproduction stage. The normal *Cutleria* is said to have been gathered at Helgoland by WOLLNY, but has not been known to occur there since. The origin of the plant is not clear.

The cultures of *Cutleria* and *Aglaozonia* made by CHURCH in 1898 were from material collected in English waters. CHURCH (**6**) obained the material by dredging in the estuary of the river Yealm, near Plymouth, England, at 2–3 fathoms below low water

mark. The male plants of *Cutleria multifida* were very rare, and in cultures of the female gametes there was produced parthenogenetically a form identical with the form *Falkenbergiana*. Further, from the zoospores of *Aglaozonia parvula* CHURCH obtained plants which, like the preceding, have the creeping platelike thallus of *Aglaozonia*, but whose column ends at the summit in filaments (not fascicled) which bear the male gametangia of *Cutleria*. The latter, being entirely a new form and having never been obtained by any previous investigators, may be designated as form *Churchiana*. Finding that the female gametes develop parthenogenetically and the zoospores of *Aglaozonia* produce *Aglaozonia* directly with no alternating appearance of *Cutleria*, CHURCH concludes that *Cutleria* and *Aglaozonia* represent simply polymorphism due to environmental conditions, especially such as changes in the temperature of water.

In 1898 SAUVAGEAU (**43**) reported that he found in nature, epiphytic upon adult *Cutleria adspersa*, a number of young sporelings of the same species. These sporelings were of two kinds, forms *Thuretiana* and *Falkenbergiana*, which were evidently growing side by side, at the same time, and on the same spot under similar conditions. In the summer of 1898, KUCKUCK (**25**) obtained in cultures at the Helgoland Laboratory a number of young plants germinating from the zoospores of *Aglaozonia parvula*. The young plants had the characters of the form *Thuretiana*, and in his material female gametangia of *Cutleria* were produced. Besides, some of the plants produced a creeping disk, so that the whole structure resembled the form *Churchiana*, but the form *Falkenbergiana* never appeared.

SAUVAGEAU (**44, 45**) found at several points on the coast of the Gulf of Gascony, France, a new *Aglaozonia*, the *Zonaria melanoidea* Schousboe, discovered at the beginning of the century at Maroc and not reported since, whose *Aglaozonia* nature remained unrecognized. SAUVAGEAU considers *Aglaozonia melanoidea* to be the sporophyte of *Cutleria adspersa*. In cultures of *Cutleria adspersa* which he collected at Guéthary (Basses-Pyrénées), he observed that the female gametes did not attract the male gametes. The female gametes germinated very readily parthenogenetically and

gave always and characteristically the form *Falkenbergiana*. In 1905 SAUVAGEAU (**47, 48**) collected *Aglaozonia melanoidea* at Banyuls-sur-Mer (Pyrénées-Orientales), and in winter and early spring in each successive year of 1905–1908, he (**46–51**) carried on his cultures at the Laboratory Arago, Banyuls. From the zoospores of *Aglaozonia melanoidea* he obtained, in a majority of cases, *Cutleria adspersa*, and in only one case out of 100 did he obtain *Aglaozonia melanoidea;* but neither the form *Churchiana* nor the form *Kuckuckiana* was produced. Unfertilized female gametes of *Cutleria adspersa* produced either *Aglaozonia* or *Cutleria*.

From his own results and those of previous investigations, SAUVAGEAU concluded that the alternation of two generations is not necessary, but rather, as it might be said, facultative. OLTMANNS (**35**), from results of previous authors, considers *Cutleria* as presenting no true alternation with the *Aglaozonia* generation, but as simply presenting another instance of polymorphism in algae. STRASBURGER (**59**), discussing the alternation of generations in Phaeophyceae, agrees with the views of SAUVAGEAU and OLTMANNS.

All these investigations, discussions, and conclusions were made without any reference to nuclear conditions. The cytology of *Cutleria* and *Aglaozonia* was first described by the author as a preliminary note three years ago (**74**).

The material for the present investigation was collected at the Bay of Naples in the winter of 1908 and spring of 1909, during which time I occupied a table of the Carnegie Institution at the Stazione Zoologica. *Cutleria multifida* was found growing on rocks at a depth of 1–5 meters in the vicinity of Posilipo and Castello dell 'Uovo, and *Aglaozonia reptans* was growing on the surface of echinoderm shells or stones in the same localities and also at Nisida along the Bay of Naples, often at a greater depth. A fresh and plentiful supply of material was furnished by Dr. SALVATORE LO BIANCO almost every day. Cultures of the plants and of their sporelings and the fixation of their critical stages were made in the laboratory of the Station, where by the kindness of Drs. ANTON DOHRN and REINHART DOHRN the author enjoyed every equipment for facilitating the work. The investigation thus begun at Naples was finished at the Hull Botanical Laboratory of the University of

Chicago. To Professor JOHN M. COULTER and Professor CHARLES J. CHAMBERLAIN I wish to express my thanks for their suggestions and criticisms throughout the investigation.

The paper presents the results of my studies on *Cutleria* and *Aglaozonia*. For *Cutleria* there is described the mitosis in the vegetative cells of the male and female plants, the formation of the male and female gametes, the fertilization and the germination of the fertilized female gametes, and the germination of the unfertilized female gametes; for *Aglaozonia* the mitosis in the vegetative cells, and the formation and germination of the zoospores. Finally, there is a brief discussion of the cytological phenomena and the alternation of generations.

Cutleria multifida

Cutleria multifida J. Ag. is generally dioecious, and the forms of the male and female plants vary with the localities in which they grow. At one place, the male plants are more broadly multifid and shorter than the female, which are very narrowly multifid and often reach a length of 25 cm. or more; in other localities the reverse is true, that is, the male plants are narrowly divided and larger than the female plants. An extensive comparative study of the forms shows that there is great variability in habit, so that it seems impossible to distinguish the two mature sexual individuals by any gross morphological aspects, except that they bear, as a rule, exclusively either male or female reproductive organs. *Cutleria* grows in the Bay of Naples upon rocks or mollusk shells, at a depth of 1–5 meters. The *Cutleria* material was collected with the rocks or shells upon which it was growing, and there was always an abundant display of the successive stages in the development of the plants, from the very young thallus to large adult forms. The young thallus is 1–3 mm. in length, narrowly funnel-shaped, and presents no feature to distinguish the male plants from the female.

MITOSIS IN THE VEGETATIVE CELLS OF THE MALE AND FEMALE PLANTS

Both male and female plants, when fresh, always bear a beautiful fascicle of hairs at the tips of the multifid filaments of the thallus, and scattered here and there upon the whole surface of the thallus

there are also tufts of hairs. Any part of the frond in vigorous growth is favorable for the study of vegetative mitosis, but details are more easily and definitely followed in the hairs and in the superficial layer of the thallus.

The cells in these regions are full of plastids, with usually a single nucleus in the center. The nucleus in the resting stage is very

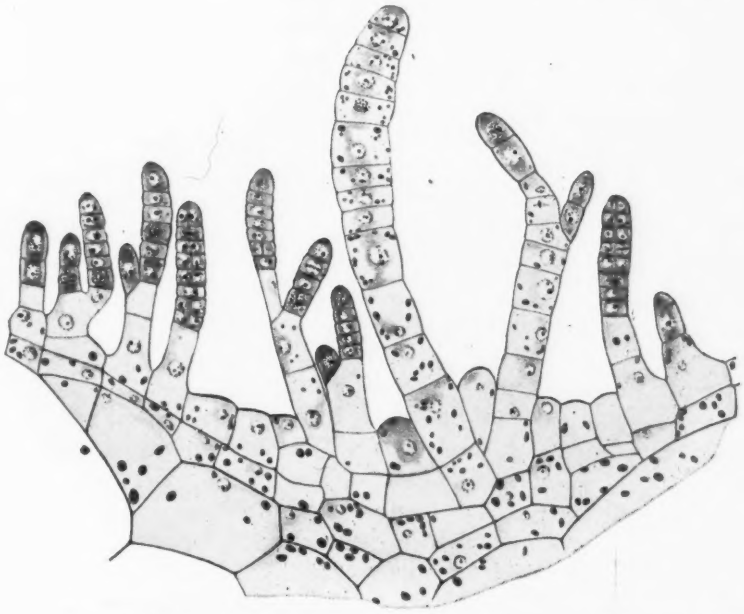


FIG. 1.—*Cutleria multifida:* portion of a thallus with a number of filaments and young male gametangia.

small, generally about the size of the plastids or slightly larger (figs. 1, 5, 16, 53). The network is so fine that it is hard to recognize much chromatin in it. Neither centrosome nor central bodies with or without radiations seem to be present.

In early prophase the nucleus increases in size, until it becomes three or four times the diameter of the resting nucleus and is a conspicuous structure within the cell. During the growth of the

nucleus, just inside the membrane, there appear chromatin knots which are evidently worked out of the chromatin network by the rearrangement of the material. These chromatin knots, which are continuous with less deeply stained chromatin fibrils, are variable in number at first, but gradually the number of chromatin knots becomes definite and they are detached entirely from the chromatin fibrils and become the chromosomes, 24 in number (figs. 19, 54). The chromosomes, after segmentation, gradually assume a slightly elongated rod form and become arranged at the equatorial plate (figs. 20, 55).

A little before the equatorial plate stage, from the cytoplasm surrounding the nuclear membrane, kinoplasmic accumulations arise at the poles. A well marked centrosome-like structure in the kinoplasmic masses occurs only at the metaphase. The chromosomes split longitudinally and half of each chromosome proceeds to each pole (figs. 22, 56). During this entire process the spindle is intranuclear. At telophase the nuclear membrane disappears and the two sets of daughter chromosomes, crowded closely together, are surrounded by cytoplasm, and the formation of the nuclear membrane follows (figs. 28, 57).

When the daughter nuclei are organized, the central spindle disappears completely (figs. 29, 57). The cytoplasm lying between the two nuclei begins gradually to assume a coarse, irregular, alveolar structure, and the walls of the alveoli, probably after a change in their material, form a new cell plate. Vegetative mitosis is essentially the same in both male and female plants.

The size of the nucleus varies according to the portion of the thallus in which the nucleus is contained. The hairs and superficial cells contain larger nuclei than the huge cells situated below the superficial cells; however, even those in the hairs and superficial cells vary in size. There seems to be no relation between the size of the nucleus and that of the cell. Quite frequently the narrow cells in the hairs contain larger nuclei than the elongated cells; usually the marginal cells in the superficial layer of the thallus have larger nuclei than the others. On the whole, the nuclei of the female plants are slightly larger than those of the male plants. However, such a difference, if it exists, is not very great during the vegetative

division, but the conspicuous difference in size appears in the formation of the reproductive organs.

THE MALE GAMETANGIUM

Mature male gametangia.—Male gametangia occur all over the surface of the thallus in small or in large clusters (figs. 1, 2, 3, 4). When the male plant is young, before the appearance of gametangia, the surface of the thallus bears tufts of hairs here and there in somewhat regularly scattered spots. Later, with or without the association of the hairs, young male gametangia appear. Both the male gametangia and hairs arise from superficial cells of the thallus.

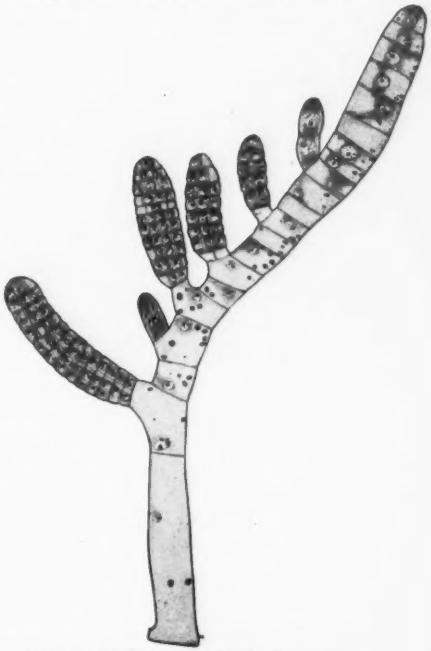
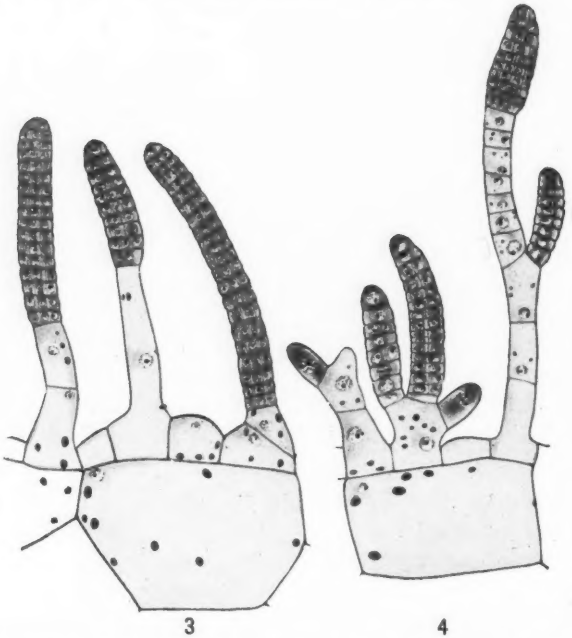


FIG. 2.—*Cutleria multifida:* a filament bearing a few male gametangia in successive stages of development.

The mature male gametangium consists of a number of tiers of small cells (the male gamete mother cells), each tier composed of 8 cells, and since there are more than 22 tiers (fig. 4), the output of male gametes from a single gametangium is about 200. The mature male gamete in the free swimming condition outside of the gametangium has an oval shape (fig. 8, *a*) and usually contains two plastids. Associated with one of the plastids, inside of the lateral face of the plasma membrane near the anterior end, is a red pigment, and in close association with this pigment are two cilia of different lengths, the long cilium directed toward the anterior end, 4.5 times the long diameter of the gamete, and the short one in the opposite direction, about twice the diameter of the gamete. The long diameter of the entire male gamete is 5 μ (figs. 3 and 4).

Development of male gametangia.—As was stated above, both the hairs and gametangia arise from the superficial cells of the thallus.

One of the superficial cells commences to grow more vigorously than the rest (fig. 17) and a typical nuclear division takes place, which gives rise to a gametangium initial and a stalk cell. Some-



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FIGS. 3, 4.—*Cutleria multifida:* fig. 3, one of the male gametangia, with a long stalk composed of several cells; fig. 4, gametangia near maturity; one of them has 22 tiers of mother cells.

times 2–7 or more subsequent divisions occur and there is produced a filament of two or more cells, the terminal one of which is destined to be a male gametangium initial (figs. 1, 3, 4). Or a filament becomes a long multicellular structure of a single row of cells, and from a number of these cells there are produced lateral branches, consisting of one, two, three, or more cells, the terminal one of which becomes the gametangium initial (figs. 2, 21, 39).

The nucleus of the male gametangium initial is considerably larger than is common in cases of vegetative mitosis (fig. 18). The chromatin network of the resting nucleus is marked by a number of knots mixed with broken fibrils (fig. 18). The chromatin knots increase gradually in size in prophase and finally break up into 24 chromosomes (fig. 19). Up to this stage the nucleolus remains without apparent change. When the chromosomes begin to be arranged at the equatorial plate, the nuclear membrane becomes contracted, and at the completion of the nuclear figure the decrease of the diameter of the nucleus is remarkable (fig. 20). Two distinct centrosome-like structures now are present at metaphase. While the nuclear membrane still persists, the chromosomes split longitudinally and half of each chromosome proceeds to each pole (fig. 22). The nucleus passes into telophase, two new daughter nuclei are formed, and then the subsequent divisions occur. In the second division the two nuclei may undergo mitotic changes simultaneously, both showing 24 chromosomes in prophase (fig. 23), or one may proceed more rapidly than the other. Figs. 24 and 25 show the latter case; the nucleus of the upper cell is in prophase, showing 24 chromosomes, and that of the lower cell is in metaphase. In figs. 24 and 25, in spite of the apparent similarity in the size of the lower cells, the difference in the size of their nuclei at metaphase is remarkable. Sometimes the nucleus of the upper cell is far behind that of the lower cell in dividing, so that, as in fig. 26, the upper nucleus is in the resting condition while the lower one is in anaphase. Fig. 27 shows the nucleus of the upper cell in metaphase, which passes to anaphase (fig. 28) and to telophase (fig. 29) while that of the lower cell remains resting. When the filament has reached the 3-celled stage mitosis in the three nuclei proceeds in varying order. In fig. 30 is shown the case in which the nucleus of the basal cell is more advanced, revealing 24 chromosomes in prophase. The following figure shows the nucleus of the terminal cell in advance and now in metaphase. In the next figure the nucleus of the middle cell is already in anaphase.

At the 4-celled stage of the young gametangium, the nucleus in prophase invariably shows 24 chromosomes (figs. 33, 34). At about this stage the nucleus in division has almost the same size and

aspect as the nuclei in vegetative filaments. In figs. 35 and 36 are given anaphase and prophase of the vegetative division. Until about the 4 or 5-celled stage the young gametangium consists of a single row of cells, after which division also occurs perpendicular (figs. 37, 48) to the direction of the axis of the gametangium, so that there are two rows of cells. When the young gametangium has reached the 8 or more-celled stage and consists of two rows of cells, the nucleus in both the resting and dividing condition has necessarily been forced to assume a somewhat irregular form so as to occupy the largest possible space, and it does not decrease much in size in spite of the multiplied divisions and consequent diminution of the cells of the gametangium (figs. 40, 41).

Another division perpendicular to the direction of the growth of the gametangium occurs (figs. 42, 44), and the gametangium becomes a structure composed of four rows of cells. The diminution in the size of the nucleus is now recognizable (figs. 43, 45). Although the chromosomes which appear in prophase are 24 in number, their size has become remarkably reduced to about half the diameter of those appearing in earlier mitoses. The diminution may proceed still further during the divisions which multiply the number of the cells in a tier. There now occurs the third and last division perpendicular to the axis of growth of the gametangium (fig. 50), resulting in a structure composed of eight rows of cells. Even after the gametangium shows eight rows of cells, a number of mitoses may occur that increase the number of cells in the rows (figs. 46, 47, 48, 49), and during these mitoses there are always 24 chromosomes. These longitudinal divisions of the gametangium, as well as the transverse, are strictly simultaneous, but they proceed at a nearly uniform rate, so that ultimately there is formed the well known male gametangium of *Cutleria*, which is composed of eight rows of cells, each row made up of a varying number of cells. The number of cells in a row may be even more than 24, the cells of each row lying side by side with the cells of the contiguous row. Each individual cell in the gametangium is a male gamete mother cell, within which a single male gamete is formed.

The mother cell contains a single large nucleus situated in the

center, and usually two plastids whose position varies. The nucleus passes into a completely resting condition. Fig. 52 represents a cross-section of a male gametangium, each gamete mother cell showing a red pigment spot in close association with the nucleus. When the male gametes are mature within, a portion of the free surface of the membrane of the mother cell dissolves so as to leave a small pore, through which the gametes are discharged. The cilia of the gametes first protrude from the pore, keep moving for a while, and then all the contents emerge and the male gamete is set free.

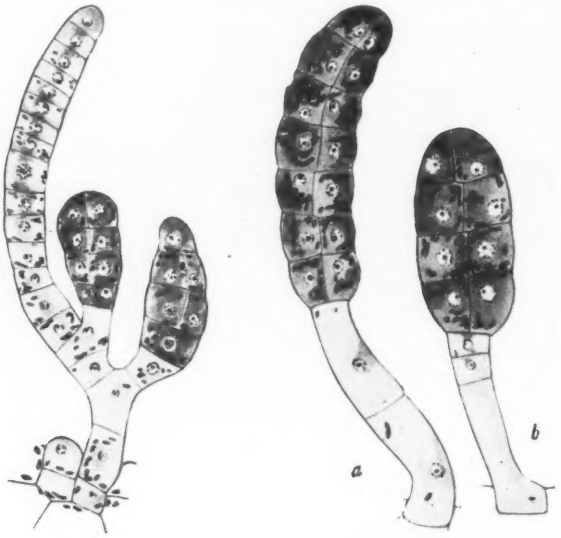
FIG. 5.—*Cutleria multifida:* portion of a thallus with a number of filaments bearing female gametangia in various stages of development.

THE FEMALE GAMETANGIUM

Mature female gametangia. — Female gametangia are scattered over the whole surface of the thallus, as in the case of the male gametangia (figs. 5, 6, 7). The female gametangia are developed alone or are associated with hairs which appear upon the surface of the thallus long before the appearance of the gametangia. As in the case of the male plants, the hair and gametangium originate from superficial cells of the thallus.

The mature female gametangium consists of several tiers of female gamete mother cells, the number of tiers varying from 4 to 7. Each tier is composed of 4 or 8 mother cells, so that the output of gametes from a single female gametangium fluctuates between 16 and 56. The mature female gamete in the free swimming condition outside of the gametangium is oval (fig. 8, *b*), and usually contains more than 30 plastids. The anterior end of the body of the female gamete is destitute of plastids and contains colorless granular

cytoplasm, thus indicating the existence of polarity in the distribution of plastids. In association with one of the plastids, which is situated near the periphery in the vicinity of the anterior end, there is present a red pigment spot. Close to the pigment spot, two cilia of unequal length are borne; the long one being directed toward the anterior end, 1.5 times the long diameter of the gamete, and the short one in the opposite direction about equal in length to the



6 7

FIGS. 6, 7.—*Cutleria multifida:* fig. 6, a filament bearing two female gametangia; fig. 7, female gametangia near maturity; *a* consists of 7 tiers of mother cells, and *b* of 4 tiers.

diameter of the gamete. The long axis of the female gamete is 26.2 μ. The female gamete is actively motile when discharged, but after a while the movement becomes sluggish, the shape becomes spherical (fig. 8, *c*), and the cilia are withdrawn.

Development of female gametangia.—Like the male gametangium, the female gametangium arises from a superficial cell of the thallus. One of the superficial cells begins to grow more rapidly than the others (fig. 53) and a typical mitosis takes place, which gives rise

to a gametangium initial and a stalk cell. Sometimes a second or third division is intercalated between the first division occurring in the superficial cell and the formation of the gametangium initial, and in this case the female gametangium, instead of having a stalk of a single cell, has a stalk consisting of two (fig. 7, *a*) or three cells (fig. 7, *b*). Or a number of divisions follow the first, so that the superficial cell develops into a long filament and some cell of the filament divides laterally to form a branch which becomes a gametangium initial (fig. 6).

The nucleus of the gametangium initial increases greatly in size, as in the case of the male gametangium initial. In it there is contained a large number of plastids. The chromatin network of the nucleus, which is composed of irregular knots and scanty fibrils during the resting stage, gradually increases in chromatin content, and finally there is established a prophase (fig. 54) containing 24 chromosomes and a single nucleolus. In metaphase the volume of the nucleus diminishes considerably (fig. 55), when compared with the previous stage, and centrosome-like structures appear at the poles. While the nuclear figure is still intranuclear, the chromosomes split longitudinally and half of each chromosome passes to each pole (fig. 56). At telophase two daughter nuclei are formed, and no central spindle remains between them. The cell plate is laid down by the cooperation of the vacuoles and rearrangement of the cytoplasm (fig. 57). Each nucleus of the two cells grows in size simultaneously during the resting condition (fig. 58) and then the rates of the mitotic processes in these two nuclei diverge; the upper nucleus enters prophase, showing 24 chromosomes (fig. 59),

FIG. 8.—*Culleria multifida:* gametes sketched from living material; *a*, male gamete; *b*, female gamete; *c*, female gamete which has become quiescent and spherical; *d*, female gamete germinating apogamously.

metaphase with two centrosome-like structures (fig. 60), anaphase (fig. 61), and reaches telophase (fig. 62) while the lower nucleus still remains in the resting condition. Sometimes the lower nucleus divides first, showing metaphase with two centrosome-like structures (fig. 63) and anaphase (fig. 64) while the upper nucleus rests.

In the young female gametangium, consisting of three cells, the mitoses occur in varying order; sometimes the nucleus of the basal cell divides first (figs. 65, 66), sometimes that of the upper cell (figs. 67, 68), and sometimes that of the middle cell (figs. 69, 70), and during these divisions 24 chromosomes are always seen in prophases (figs. 65, 66, 69, 71).

Up to the 4-celled stage the female gametangium divides transversely, and then a perpendicular division occurs (fig. 72), so that the gametangium consists of two rows of cells, after which another longitudinal division (figs. 73, 78) immediately follows and results in producing a gametangium of four rows of cells.

Mitosis in the gametangium of the 7–11-celled stage is not simultaneous, but occurs at different times in different cells. The nucleus in the middle cell may divide ahead of the others (figs. 74–77, 79, 80, 83, 84), whose nuclei are either in the resting stage or in prophase. The nucleus in prophase in any of these cells always presents 24 chromosomes, and in metaphase two centrosome-like structures are seen at the poles. It is remarkable that the chromatin knots or globules in the resting nucleus always lie quite independent of one another, the chromatin fibrils being so scanty that they are unable to connect them together.

In the young gametangia of the 10–18-celled stage, the mitoses take place as in earlier stages (figs. 85–88); the prophase and the polar view of metaphase show clearly that the number of chromosomes is 24. One striking feature as contrasted with the male gametangia is that in the female gametangia the nuclear diminution in size is not very great during the repeated divisions and consequent multiplication of cells of the gametangia. Of course the nucleus at the time of the first division in the female gametangium is rather large, especially in prophase (fig. 54), and the nucleus in the prophase of the division in the female gametangium of the 18-

celled stage is almost two-thirds of that diameter (fig. 87), but if the nuclei in metaphase and in the resting condition are taken into consideration, almost all of the cases in the gametangia from the 2-celled stage to 18-celled stage seem alike. The female gametangium, consisting of four rows of cells, becomes mature (fig. 89), but quite often each of the cells in the four rows divides again, so that the gametangium consists of eight rows of cells (fig. 90).

These numerous nuclear divisions are not simultaneous, but follow in regular order, both those which are transverse to the axis of the gametangium and those which are perpendicular to it, so that the ultimate result is the well known female gametangium of *Cutleria*, which is composed of four or eight rows of cells, each row composed of 4–7 cells, the cells of each row lying almost exactly opposite the cells of the neighboring row. Each individual cell of the gametangium is a female gamete mother cell. The mother cell contains a large nucleus either in the center or near the inner wall (figs. 90, 92). Plastids are crowded either near the inner wall (fig. 91) or near the outer side (fig. 92), or lie scattered regularly throughout the whole cytoplasm. The nucleus is in the resting condition.

When the gametangium is mature, the whole contents of a gamete mother cell become a single female gamete. A portion of the free surface of the mother cell dissolves and forms a pore through which the gamete is discharged. The slow process of discharging the gametes is the same as in the case of the male gametes; first, the cilia of the gametes appear outside the pore, keep waving for a while, and then the female gamete is set free.

FERTILIZATION AND THE GERMINATION OF THE FERTILIZED FEMALE GAMETES

The discharge of both male and female gametes occurs at almost any time during the day and night. However, so far as the writer's experience goes, while he was making observations at half-hour intervals under the microscope, the majority of cases showed that the discharge was most abundant at 5 A.M., and that it continues, though gradually diminishing, until 7 A.M. and then ceases. Occasionally there is some discharge at 11 A.M. and 5 P.M. The motile

power of the male gametes continues for almost 20 hours, while that of the female gametes is comparatively short, the longest period of the swimming condition observed having been 2 hours, and the shortest 5 minutes. Toward the end of the motile condition in both male and female gametes, the movements become sluggish, and then cilia are no longer recognizable, seemingly being withdrawn or coalescing with part of the plasma membrane of the gamete body, and finally the shape of the body becomes spherical. However, in a number of cases gametes caught in the thallus of algae while swimming between the slide and cover-glass remained active for more than 24 hours, and then became spherical; when stained at that time they showed the cilia still persisting and not coalescent with the plasma membrane.

The union of male and female gametes and the subsequent nuclear behavior were studied in material from artificial cultures. A number of dishes were prepared containing either male or female plants bearing mature gametangia. When the discharge of gametes became abundant, the sea water of the dish containing thousands of swarming male gametes was added to a dish containing vigorous female gametes. Then part of this mixture was observed under the microscope in living condition and part was fixed every 30 minutes for 24 hours, and then at 26, 28, 32, and 48 hours, and later, every 3 or 5 days up to 75 days. The following description is based upon material obtained in this way.

The male gametes while swimming freely become attached to the female gametes which are either sluggishly swimming or have come to rest, but have not yet formed a cell wall. When the male gamete becomes quiescent, before coming in contact with the female gamete it withdraws its cilia and its shape becomes spherical. The nucleus is full of chromatin which is clearly broken into 24 independent chromosomes. The nuclear membrane is very delicate (fig. 94). When a male gamete has just become attached to the female gamete, both gametes have very delicate plasma membranes. The nucleus of the female gamete is at the center of the cell, as in the resting condition (fig. 95).

Then the plasma membranes which lie between the cytoplasm of the male and female gametes become obscure and the cytoplasm

of the two gametes comes into direct contact. The male gamete can be observed for a short time as a protuberance at the periphery of the female gamete (fig. 95); however, sooner or later the protuberance is entirely absorbed or leveled down to the surface of the now spherical female gamete. The male nucleus with 24 distinct chromosomes proceeds toward the resting female nucleus (fig. 96); it then proceeds still further (fig. 97) until it is close to the female nucleus (figs. 98, 99). The male nucleus at this stage is surrounded by a clear zone, which possibly means that the nucleus is carrying with it a part of the male cytoplasm or a part of the female cytoplasm which had been lying in the path of the male nucleus. The male nucleus now becomes closely applied to the female nucleus (fig. 100). The chromatin of the male nucleus becomes closely aggregated (fig. 101), and then begins to be finely alveolated (fig. 102), and finally becomes dispersed through the female nucleus as irregular knots (fig. 103). Later the fusion nucleus contains chromatin knots of various sizes and shapes, together with delicate, irregular, discontinuous fibrils. A nucleolus which was present in the female nucleus before the union still persists (fig. 104). The fusion nucleus thus passes into a completely resting condition, in which chromatin of male and female origin cannot be distinguished from each other.

Returning to the previous stage, at the time of the union both gametes are surrounded by plasma membranes only. At the time of the entrance of the male nucleus into the female cytoplasm the outermost layer of the plasma membrane is observed to change into cell wall (fig. 96), which is very thin at first, but gradually increases in thickness as fusion progresses, and is well organized by the time the fusion nucleus reaches the resting condition.

The first segmentation division of the sporelings of the fertilized gametes takes place 20–24 hours after the union of the gametes. In prophase there appear 48 chromosomes, all of which seem alike both in size and shape (fig. 106), and a single nucleolus persists. At metaphase the chromosomes are arranged at the equatorial plate and two centrosome-like structures appear at the poles (fig. 107). A comparison of the prophase and metaphase shows that the volume of the nucleus is considerably diminished at the

latter stage. The mitosis may take place before the sporeling begins to elongate; but in the majority of cases the sporeling elongates into a somewhat pear-shaped structure while its nucleus is still in the resting state (fig. 108). Quite often the nucleus is present at the elongated portion (fig. 109). The cell wall of the elongated portion which is to become the holdfast is comparatively thick.

The number of chromosomes at prophase (figs. 110, 111) and seen in polar view at metaphase (fig. 114) is 48. The axis of the figure is often perpendicular to the growing axis of the sporeling (fig. 113). After telophase the sporeling is divided into two cells (fig. 115). The nuclei of the two cells divide one after the other; sometimes the lower nucleus increases more rapidly than the upper (fig. 117), or the upper nucleus begins to divide first (figs. 116, 118–120). In sporelings consisting of three cells, mitosis occurs in various order in the three nuclei; the nucleus of the basal cell may divide first (figs. 121, 122), or the three nuclei may divide simultaneously (fig. 123). The number of chromosomes appearing at the prophase (figs. 121, 123) is 48.

The fourth, fifth, and subsequent divisions, that occur continuously for more than ten days, multiply the number of the cells of the sporeling, resulting in the development of the upright columnar form that grows standing upon the substratum, and then the direction of growth becomes changed.

Before describing this change of growth which occurs in sporelings about ten days old, we shall note briefly the fate of the red pigment that is conspicuous in the living gametes. As was stated before, the red pigment is always associated with the plastid. A part of the plastid becomes impregnated with some substance of a deep orange color, which seems to disorganize instantly with the death of the sporeling. The most interesting point is that the cilia are attached to the pigment, and the red pigment is the only structure within the sporeling that bears any close and direct physical connection with the cilia. Moreover, the plastid that bears the red pigment always lies near the nucleus. By the union of male and female gametes the red pigment bearing plastid of the male gamete is introduced into the female gamete and consequently

two red pigment structures are always present in sporelings resulting from fertilization: a large red pigment spot is associated with a large plastid of the female gamete, and a small red pigment spot upon a small plastid is characteristic of the male gamete. Although the plastid bearing the red pigment of the male gamete grows in size after its introduction into the cytoplasm of the female gamete, yet it seldom becomes equal in size. This difference in size of the two pigment spots is maintained as far as the present observation goes. Fig. 9 represents some of the stages in the development of sporelings from the 1-celled to the 5-celled stage, indicating the various positions of the two red pigments of male and female origin. The red pigment was recognizable even up to the 16-celled stage, and beyond the 20-celled stage it becomes hard to recognize, probably on account of the disintegration of the coloring matters. It seems probable that the red pigment is concerned with the motility of the gamete rather than with fertilization.

As stated before, the sporelings develop continuously in one direction, and as a consequence after about ten days there is produced a columnar structure standing upright upon the substratum, and then the direction of the growth becomes changed. Cells of the basal portion of the columnar sporeling divide laterally, instead of in the direction of the axis of the growth, so that by repeated cell division there is produced a flat expansion, the whole structure of which might be well compared with a candlestick, the candle being the column and the base the newly developed flat expansion. The basal expansion is developed by the repeated periodic cell divisions on the lateral margin, which causes a zonation like that in *Peyssonnelia;* besides, the thallus is characterized by intercalary growth. Sporelings at about 20 days after fertilization are shown in fig. 10, *a*. Later the upright column does not seem to grow much, only the basal expansion continuing to develop. Sporelings 30 days old are shown in fig. 10, *b*. In 55 days old sporelings, the growth of the column has ceased, and it remains small, hardly recognizable to the naked eye, while the basal expansion reaches a considerably larger size and becomes well fitted to flourish as an independent creeping structure (fig. 10, *c*, *d*).

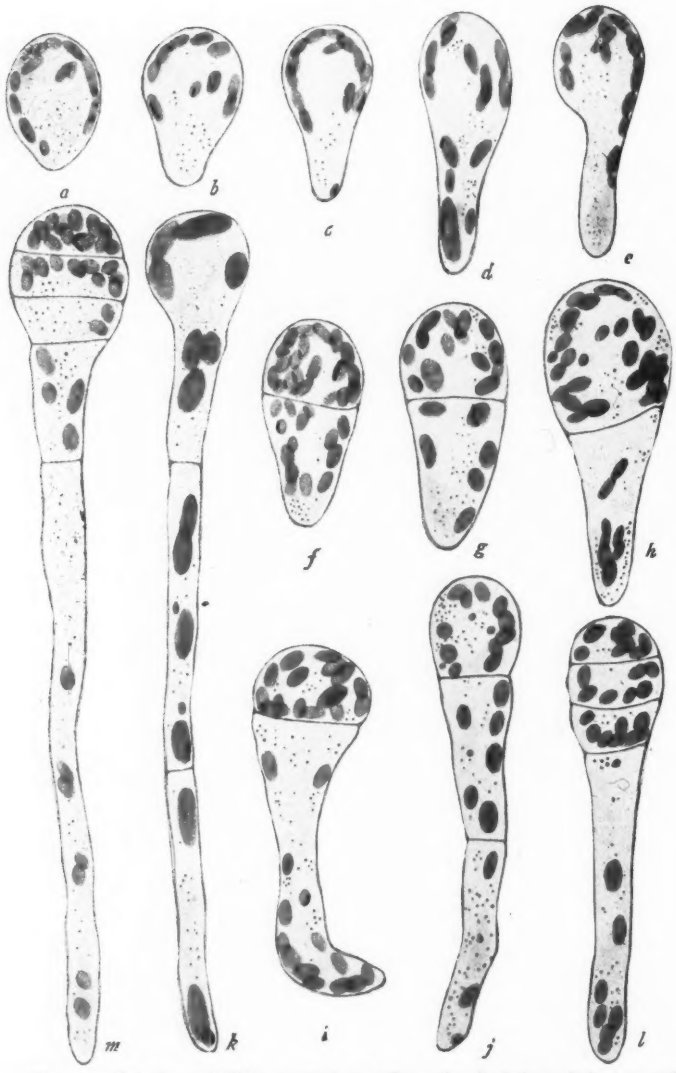


FIG. 9.—*Cutleria multifida:* normal sporelings sketched from living material; *a–e*, one-celled stage; *f–i*, two-celled stage; *j* and *k*, three-celled stage; *l*, four-celled stage; *m*, five-celled stage; nucleus not recognizable in living material; the two pigment spots associated with plastids are of maternal and paternal origin; the small pigment spot introduced by the male gamete, the large one by the female gamete; the plastid that bears the small red pigment spot has increased in size after its introduction into the female gamete.

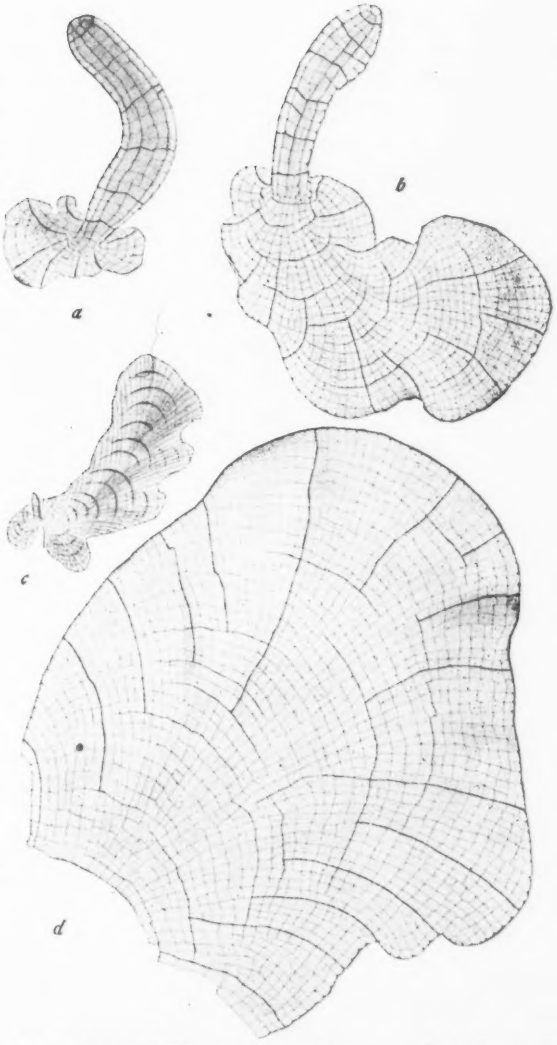


FIG. 10.—*Cutleria multifida*: normal sporelings; *a*, 20 days after fertilization; *b*, 30 days after fertilization; *d*, 55 days after fertilization (*d* represents a part of a sporeling under the same magnification as *a* and *b*, and the whole sporeling is shown in *c*); the vertical column which is the result of primary growth of the sporeling has not grown since 30 days after fertilization, and the zonal horizontal expansion at the base of the column begins as a secondary structure and develops into the characteristic *Aglaozonia* form, as shown in *b* and *c;* compare with fig. 11.

The similarity of the habit of this creeping expansion of the thallus to that of *Aglaozonia* in nature is striking. The material of *Aglaozonia* collected fresh from Posilipo and Nisida, which has grown creeping on a sea-urchin's shell or on the rock, showed a number of forms in various stage of development. If the creeping expansion of the thallus obtained in cultures is compared with *Aglaozonia* of similar size as it occurs in nature, it is hard to find any difference in their appearance. Not only the zonal growth and occasional intercalary growth of the thallus is alike in these two forms, but also the cell structure as seen in sections under the microscope is remarkably similar in the two forms. The nuclei of the thallus obtained in culture contains 48 chromosomes, and the same number is present in *Aglaozonia* as it occurs in nature.

The author's cultures of the thallus expansion, the *Aglaozonia* form of *Cutleria*, were not continued up to the stage of producing reproductive organs.

GERMINATION OF THE UNFERTILIZED FEMALE GAMETES

As was described before, the female gametes after their escape from the gametangia may swim for as long a time as 2 hours, or for as short a time as 5 minutes. When the motion becomes sluggish, the body becomes spherical, the plastids which have hitherto occupied the more posterior portion of the body become irregularly scattered throughout, and finally the cilia are either withdrawn or they coalesce with the plasma membrane as the movement ceases. If the female gametes in this condition are kept with no addition of the male gametes, they remain dormant for a considerable time. The female gamete left in this condition at length shows a change in the outermost layer of the plasma membrane that is in direct contact with sea water, the change resulting in the development of a cell wall, thin at first, and then increasing in thickness. The nucleus is in the resting condition (fig. 124). Not infrequently it is observed that the female gamete, now inclosed within a cell wall, has an elongation at a part of the body where the cell wall is thickened (figs. 125, 8, *d*).

This unfertilized female gamete commences to divide 24–28 hours after it has assumed the quiescent condition. The mitosis

occurs frequently without any elongation of the sporeling. When the nucleus is in prophase there seems to be no departure from the typical mitosis characteristic of *Cutleria*, the division being perfectly normal. The number of chromosomes appearing in prophase is 24 (fig. 126). At metaphase two centrosome-like structures appear at the poles (fig. 127), and the number of chromosomes is clearly 24 (fig. 128). Sometimes the metaphase is reached while a part of the sporeling is elongating (fig. 130). The chromosomes split longitudinally and half of each chromosome passes to each pole (fig. 131). The axis of the first mitotic figure may be either longitudinal or transverse to the axis of the sporeling (figs. 132, 133). After telophase two new daughter nuclei are formed (fig. 134). In the sporeling of the unfertilized female gamete beautiful radiations are closely associated with the upper nucleus (fig. 135), but they are of short duration, and disappear completely when the nucleus passes into prophase (fig. 136). When the upper nucleus is in metaphase (fig. 137), the lower nucleus enters into prophase. Both the metaphase, viewed from pole (fig. 137), and the prophase show 24 chromosomes. One peculiarity observed is the appearance of elongated chromosomes in the upper nucleus of a 2-celled sporeling during prophase (fig. 138). The division of the upper and lower nuclei is not simultaneous; sometimes the upper nucleus is far ahead of the lower, so that the former is in late telophase

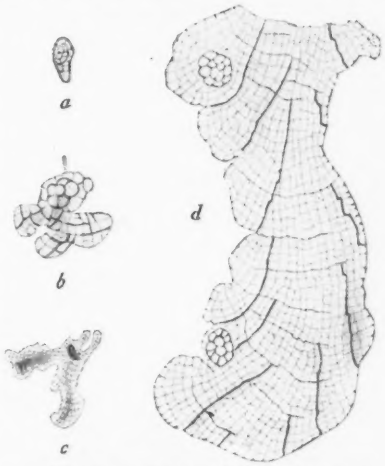


FIG. 11.—*Culleria multifida:* apogamous sporelings: *a*, 30 days after germination; *b*, 50 days after germination; *d*, 75 days after germination (*d* represents a part of a sporeling under the same magnification as *a* and *b*, and the whole of the sporeling is shown in *c*); the apogamous sporelings are slow in development as compared with the normal ones, and assume massive forms at first and then the flat zonal expansion like the normal ones.

while the latter is in metaphase (fig. 140), or the upper is left behind in the resting state while the lower is in anaphase (fig. 139). In sporelings of the 3-celled stage the lowest nucleus may divide (figs. 141, 143) in advance of the rest, or the middle one may divide first (fig. 142).

Cell divisions continue up to a 12–22-celled stage (figs. 144–146). As seen in fig. 146, the axis of growth does not continue in one direction, as in normal fertilized sporelings, but the structure is branched. After repeated divisions there is formed a somewhat upright structure, not columnar, but rather laterally produced and in irregularly massed lumps (fig. 11, *a*). This upright structure with a lateral uneven mass consisting of about 35 cells is produced in 30 days. The irregular nature of this structure is still seen in sporelings of 50 days (fig. 11, *b*). Some of the irregular appendages of the structure which happen to be in contact with the substratum become creeping expansions and later become the main part of the sporeling.

And thus the unfertilized sporelings after 75 days develop into the thalloid creeping structure (figs. 11, *c*, *d*), and the product bears some resemblance to the product of the sporeling resulting from a fertilized gamete. Comparing these two products, the points of marked difference are as follows: (1) the first segmentation division occurs 6 hours later than in the normal sporeling; (2) the subsequent growth of these sporelings is very much slower than in normal sporelings; (3) unfertilized sporelings are characterized by developing into irregular masses at first, and even after they have assumed the expanded structure, they still show a tendency to form massed appendages; (4) the number of chromosomes is unchanged, the sporeling from the unfertilized gamete containing only 24 chromosomes.

Aglaozonia reptans

MITOSIS IN THE VEGETATIVE CELLS

Aglaozonia reptans Crouan has a creeping crustaceous habit on rock or sea-urchin's shells, attached by rhizoidal holdfasts from the superficial layer of the ventral surface. The superficial layer consisting of small cells of equal size is either single (fig. 147) or

double (fig. 148) on the dorsal surface, and between the dorsal and ventral superficial layers there are two or three layers of parenchyma-like cells of huge size. Any cells in the superficial layer of the dorsal surface of young *Aglaozonia* are favorable for studying vegetative mitosis.

The vegetative mitosis was studied chiefly in the nucleus of the superficial cells of *Aglaozonia*. The main features of the division are similar to those of *Cutleria*, and consequently a detailed account and figures will be omitted at this time, but a few points should be noted.

The size of the nucleus in the superficial cells is either about the same as that of the plastids within the cell or is even smaller. When the nucleus is in the resting state, the chromatin network is remarkably similar to that of *Cutleria*, the chromatin knots being a conspicuous feature, though few in number, while the fibrils are very scanty and broken. One noteworthy feature not common in the case of *Cutleria*, but of general occurrence in *Aglaozonia*, is that deeply stained granules about the size of the chromatin knots within the nucleus are present around and close to the membrane outside the nucleus. These granules become faintly stained and evidently diminished in size during the mitotic phase within the nucleus, and they entirely disappear while the nucleus is still in prophase. It seems probable that the granules may be material allied to chromatin that might have passed into the nucleus, thus contributing to the formation of chromosomes.

The chromosomes appearing in prophase are 48 in number, and their form is in nothing different from those of *Cutleria*.

FORMATION OF ZOOSPORANGIA

Zoosporangia are produced on the upper surface of the thallus. When living *Aglaozonia* is viewed from above, the groups of zoosporangia are distinguished by patches of darker color, contrasting sharply with the light brownish olive color of the sterile portion. These patches are composed of hundreds of thousands of zoosporangia which are produced in palisade arrangement upon the thallus. The details of the origin of the zoosporangium are as follows: a superficial cell of the thallus elongates slightly and

divides, giving rise to two cells, the upper one of which becomes a zoospore mother cell, and the lower remains as a stalk cell (figs. 148, 149). The process occurs in a number of superficial cells lying side by side, and as a consequence zoospore mother cells are produced in great numbers, lying close together and parallel. When the superficial layers are double, the cells in the outer layer elongate

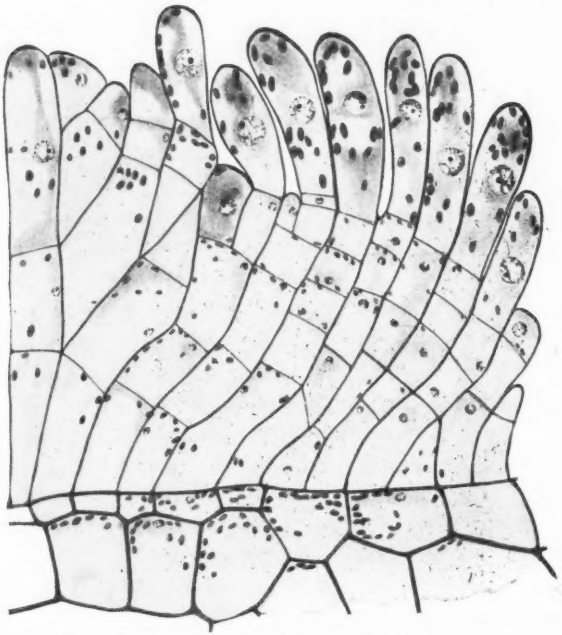


FIG. 11.—*Aglaozonia reptans:* portion of a thallus with numerous filaments; the filament usually consists of two cells, but in the present exceptional case they are made up of a varying number of cells (3–7), and their terminal cells are zoospore mother cells.

and directly become the mother cells (fig. 150). Not infrequently it is to be observed that several cell divisions take place in the superficial cells, so that a single superficial cell develops into a slender filament consisting of 3–7 cells, and the terminal one becomes the mother cell (fig. 12). The zoospore mother cell is at first like an ordinary superficial cell, with length and breadth about equal

(fig. 151), but sooner or later the cell begins to elongate upward until its length becomes three times its width, the top being slightly swollen and the base narrowed. The nucleus lies either in the center or a little above the middle of the cell. The cytoplasm is full of vacuoles of various sizes, and plastids are quite numerous.

The nucleus in the resting condition contains a moderate amount of chromatin network and a nucleolus. The network is composed of very small chromatin knots and irregular fibrils (fig. 152); the proportionate amounts of the knots and fibrils seem to interchange at this stage (fig. 153). In iron-hematoxylin preparations dark kinoplasm surrounds the nucleus (figs. 151, 152). The amount of the chromatin gradually increases and the general tendency is for the broken fibrils to become thicker and continuous, transforming the knots into the fibrils (fig. 154). At this time, a single (figs. 154, 158) or double (figs. 155, 157) centrosome-like structure with radiations is recognizable at the poles.

Stronger and more continuous threads are then established by the rearrangement of the knots and fibrils. The chromatin network, which is composed of a number of broken threads of various lengths and thicknesses, now entirely devoid of former knots, is not very great in amount. For a while the broken threads are seen running for quite a distance either close to the membrane or traversing the cavity (fig. 159, 160). Then the threads gradually become more and more uniform in thickness and are transformed into somewhat regularly arranged loops, centered at a certain part of the cavity (fig. 161). This transformation represents the beginning of the synaptic stage.

This bunch of loops may be in regular arrangement (fig. 162) or adhering at the base to the membrane and diverging upward so that each loop passes along the membrane (fig. 164); or often each loop of the bunch differs in compactness of structure, and consequently some loops are short while others extend for some distance (fig. 165). In any event, a cross-section at these stages shows that the number of the cut ends of the arms of all the loops is about 48 (fig. 166). These loops now shorten considerably (fig. 167) and some of them are soon detached from the main group and form paired chromosomes (figs. 168, 169), and finally there are established 24 bivalent

chromosomes, each derived from one of the loops (fig. 170). These 24 bivalent chromosomes gather near the center of the nucleus (fig. 171), and then are arranged at the equatorial plate (fig. 172), when the number is clearly counted in the polar view (fig. 173). Then each of the chromosomes splits longitudinally (fig. 174) and half of each proceeds to each pole of the spindle and there again the polar view of the anaphase clearly shows 24 chromosomes (fig. 175). The chromosomes grouped at the poles now become closely applied to one another (figs. 176, 177) and finally there are organized two daughter nuclei (fig. 178). Up to this phase a kinoplasmic mass persists, either surrounding the nucleus or near the pole of the spindle, but centrosome-like structures are recognizable only at metaphase.

The two newly formed daughter nuclei now increase in size. Their relative position within the cell is variable; sometimes they are wide apart (fig. 180), and often they lie for a while in close contact (fig. 182). The centrosome-like structure with radiations is present, associated with the two resting nuclei (fig. 180). These two nuclei may divide simultaneously or in succession (figs. 183–185). The number of chromosomes present during this division is also 24, and with this reduced number the nuclei pass into telophase (figs. 186–188). The third division follows the second after a short rest, 24 chromosomes being present at metaphase (fig. 189). As a result of the third division there are produced eight nuclei within the mother cell (fig. 190).

It is interesting to note the relative position of the axes of the mitoses that occurred within the mother cell. Only a few of the cases are represented in fig. 13. As the figures clearly show, the axis of the first mitotic figure is either in the direction of the long axis of the mother cell, or slightly oblique to the axis; in some cases the axis is still more oblique, until finally the axis of the figure is perpendicular to the long axis of the cell. In the second mitosis, considering the cases where the two mitotic figures occur at the same time, the relative position, as shown in figures, shows all possible directions of the axes. The same is true of the third nuclear division. All of these zoospore mother cells show no polarity in regard to the axis of the mitotic figures.

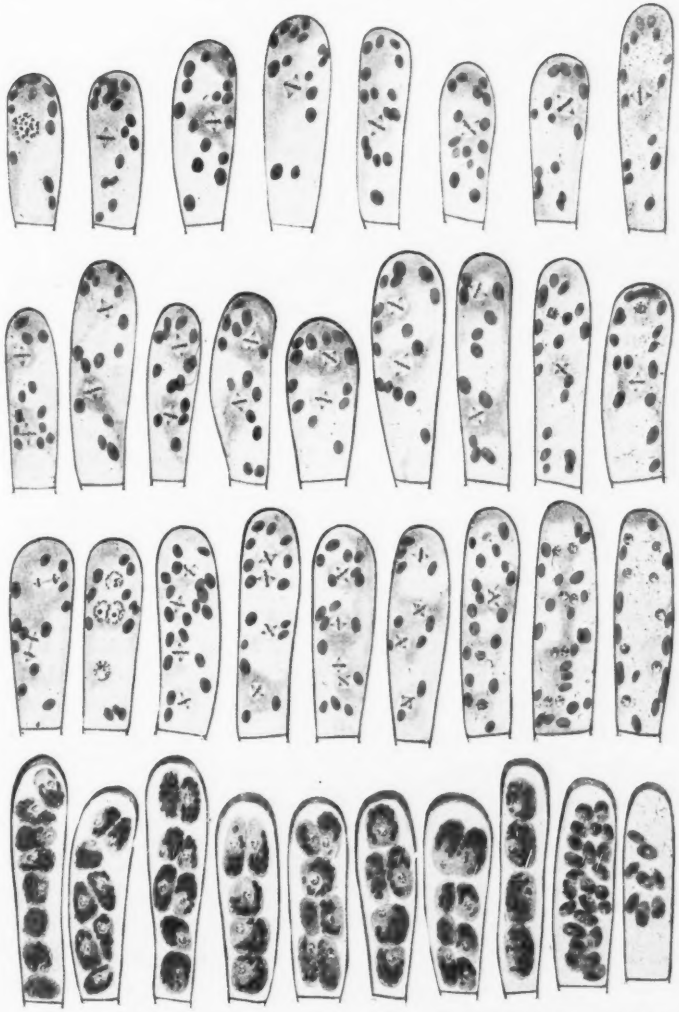


FIG. 13.—*Aglaozonia reptans:* zoospore mother cells in various stages of development; first row, the nuclear figures are in metaphase of the first division and lie in various positions in relation to the axis of the mother cell; second row, metaphase of the second division; third row, two at the right in anaphase and telophase of the second division; third row, two at the right in anaphase and telophase of the second division, two at the left in 8-nucleate stage, and the rest in metaphase of the second division; fourth row, various arrangements of zoospores formed within the mother cells, the two at the left are the two sections of a single mother cell which contains 32 zoospores, and in the rest 8 zoospores are present.

The plastids in the zoospore mother cell seem always to be multiplying in number during these nuclear divisions. When the nucleus is in prophase of the first division, the surrounding cytoplasm contains a number of plastids in various stages (fig. 191); the number is increased at the time of the 4-nucleate stage (fig. 192), and at the 8-nucleate stage the cell is filled completely with the plastids (fig. 193). It seems probable that this gradual multiplication of plastids may be one of the reasons why the zoospore mother cell constantly increases in size up to the formation of the zoospores, when the length of the mother cell becomes six times its width.

When the zoospore mother cell has reached the 8-nucleate stage, cleavage furrows generally occur in the cytoplasm, and divide the contents of the mother cell into 8 zoospore primordia (*Anlagen*). Not infrequently, however, one or two more divisions occur after the third, and as a consequence there are produced 16 or 32 nuclei, and in those cases 16 or 32 zoospores are formed (fig. 13).

The mechanism of the cleavage of the cytoplasm within the mother cell in the formation of the zoospores is noteworthy. The plastids at this time are arranged mostly near the cell membrane, and the central part of the cell is occupied by the vacuolated cytoplasm (fig. 194). The nucleus lies either near the periphery or in the midst of the cytoplasm. There is first a movement of the nuclei, and this is followed by a movement of the plastids; that is, the 8 nuclei are distributed to certain portions, not very close to the periphery, and then a number of the plastids move toward one of the nuclei as a center and surround it (fig. 195). Then there begins the separation of the *Hautschicht* from the cell wall, and at the same time cleavage furrows appear in the cytoplasm between the nuclei; the formation of the furrow is initiated by small vacuoles arranged in a cleavage line, which unite afterward and break up, leaving the furrow in their places (fig. 196). As the result of the process of the cleavage furrow, there are produced free independent zoospore primordia packed close together within the mother cell (figs. 198, 199). The relative position of the zoospores thus produced is determined by the position the nuclei had occupied before the cleavage began. Some of them are shown in fig. 13.

During the development of the zoospore mother cell, while these nuclear divisions have been taking place, the cell wall remains apparently unchanged, except at the top of the mother cell, where there has been a gradual increase in thickness, which culminates at the time of cleavage. As the zoospore primordia are completely formed, the top of the cell wall begins to swell (fig. 200), then disintegrates into lamellae, with lacunae between them (figs. 201, 202). Finally the disintegrating lamellae of the cell wall become completely disorganized, so that a pore is formed at the top, and through this the zoospores escape after maturity.

FIG. 14.—*Aglaozonia reptans:* zoospores sketched from living material; *a*, in free swimming condition; *a'*, beginning to be quiescent and spherical; *a''*, in quiescent condition; the size varies according to the number of nuclear divisions within the mother cell; *a*, *a'*, and *a''* are the products of three divisions (output of 8 zoospores); *b*, from four divisions (output of 16 zoospores); *c*, from five divisions (output of 32 zoospores).

The zoospore in free swimming condition is oval (fig. 14, *a*), and usually contains more than 20 plastids. Associated with one of the plastids, which lie inside the plasma membrane, there is a red pigment spot, in close association with which two cilia of different lengths are attached, the longer one being directed toward the anterior end, about three times the length of the zoospore, and a short one extending in the opposite direction about one and one-third the length of the zoospore. The length of the zoospore is 22.5 μ when the output of the zoospores in a cell is 8 (figs. 14, *a'*, *a''*), 18.7 μ when the output is 16 (fig. 14, *b*), and 10.5 μ when the output is 32 (fig. 14, *c*).

GERMINATION OF THE ZOOSPORE

The duration of the motile condition of the zoospores varies; some ceased to be motile within 10 minutes, while others were still moving after more than 90 minutes; but in any case, when the zoospore becomes sluggish, the body gradually becomes spherical and the cilia are withdrawn or become coalescent with the plasma membrane.

About two hours after the quiescence of the zoospore, the outermost layer of the plasma membrane becomes changed into a delicate cell wall. The nucleus at this time is in the resting condition, with a centrosome-like structure and radiations near the nuclear membrane (fig. 203). This condition remains unchanged during the next 20 hours (fig. 204). The presence of centrosome-like structures and radiations is not a definite feature; at about 24 hours after quiescence they may (figs. 206, 207) or may not be visible (figs. 205, 208).

The first segmentation division of the germinating zoospore takes place 24 hours after its quiescence. The nucleus enters prophase either at the center of the cell (fig. 209) or in its elongated part (fig. 210), and when the chromosomes are arranged at the equatorial plate (figs. 211, 213), two centrosome-like structures are present at the poles. The polar view of the metaphase shows distinctly 24 chromosomes (figs. 212, 214). Each of the chromosomes divides longitudinally and half of each passes to each pole (fig. 215). The second mitosis in these two nuclei may occur in succession (figs. 217–221) or simultaneously (fig. 222), but in either case 24 chromosomes can be counted at prophase and in polar view of metaphase.

In the zoosporelings consisting of three cells the three nuclei divide in various order (figs. 224, 225), and in prophase of any nucleus 24 chromosomes are present. In the further nuclear divisions in the development of the zoosporelings the same number of chromosomes is counted. This young sporeling after a multitude of cell divisions (figs. 226–228) develops into a long filamentous structure instead of a stout column. The product at about the end of 20 days after germination is shown in fig. 15, *a*. In habit the sporeling is very like the young filamentous stage of *Cutleria*.

Later this filament does not continue in the upward direction, but there appears a new lateral structure near the basal region of the primary filament, and the whole structure clings to the substratum with rhizoids which grow from the base; thus, contrary to the behavior of the fertilized gamete of *Cutleria*, basal expansions that creep flat upon the substratum are never found. The plant at 30 days is illustrated in fig. 15, *b*, which resembles the young *Cutleria* as found in nature.

The new structure thus initiated laterally from the basal region of the primary filament grows in such a way that it finally meets the other side of the primary filament so as to form a funnel which is expanded upward and narrowly constricted downward. Upon the expanded upper margin of this funnel-shaped structure delicate hairs begin to grow. This stage is reached in about 40 days (fig. 15, *c*). These funnel-shaped structures obtained in the artificial culture present a striking resemblance to the young plants of *Cutleria* in nature as they occur in tufts on the rock or on shells. One difference is that the young plant of *Cutleria* in nature, at the same stage as the cultures in the

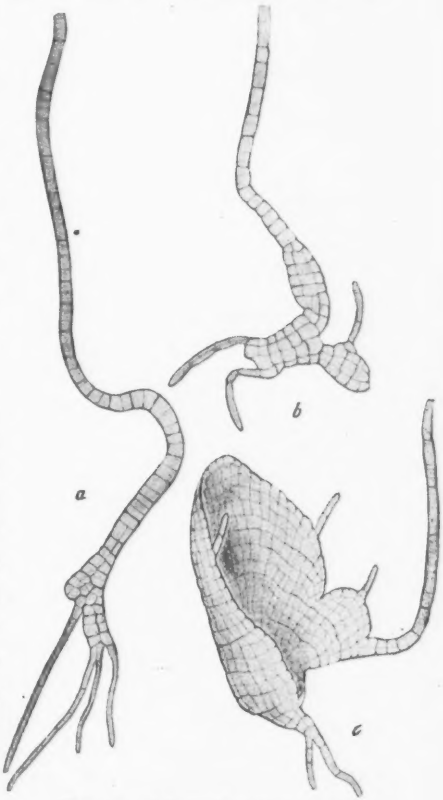


FIG. 15.—*Aglaozonia reptans:* zoosporelings; *a*, 20 days after germination; *b*, 30 days after germination; *c*, 40 days after germination; the sporelings are filamentous in primary growth as shown in *a*, then gradually assume the funnel-shape shown in *b* and *c*, this shape being characteristic of the young stage of *Cutleria* in nature.

laboratory, is furnished with a luxurious display of long beautiful hairs on the margin of its funnel-shaped thallus, while such a hairy growth has not yet been seen in cultures. It must be admitted, however, that there is a difference between conditions in nature and in cultures which may account for the difference in this character; the young plant of *Cutleria* is found on the rock at a depth of 1–5 meters, while the culture was kept in a tank where the water was never deeper than 6–8 inches. Intensity of light, temperature of water, its pressure, its movement, and other factors may be quite different, and yet in spite of such a difference of external environment, the zoosporelings of *Aglaozonia* developed into erect structures of funnel-shape as in the young *Cutleria* plants, and fundamentally different from the flat creeping expansion habit of both parent forms and of the plants resulting from fertilized female gametes of *Cutleria*.

The young plants of *Cutleria* and the product of the zoosporelings of *Aglaozonia* in culture show not only the common habit in their development and similarity in their outer morphological characters, but also a similar cell structure, similar nuclear conditions, and the same number of chromosomes.

Discussion of cytological phenomena

THE ORIGIN OF UNIVALENT CHROMOSOMES

The chief constituents of the resting nucleus of *Cutleria* and *Aglaozonia* are the network and nucleolus. The network is composed of two parts, granules and irregular fibrils in varying proportions. The granules are of different sizes and some of them are connected by very slender, irregular fibrils, or lie isolated usually near the nuclear membrane. The number of granules in the nucleus quite often, though not always, corresponds more or less to the number of chromosomes. The granules may be extremely small, but the preparations never fail to show their presence. Both granules and fibrils consist of chromatin.

As a rule, there is only one nucleolus, and it lies quite free from the nuclear network, with which it shows no visible physical connection. Concerning the morphological function of the nucleolus in algae, STRASBURGER (**55, 57**) published the view that the sub-

stance of the nucleolus is utilized for spindle formation, the conclusion being drawn from the fact that the nucleolus disappears partly or completely immediately preceding the formation of the spindle. WILLIAMS (**66**) in his study of *Dictyota* accepted this view. STRASBURGER (**53**) had held the opinion that the nucleolus was reserve material serving to build up the chromosomes, and this view was followed by SWINGLE (**61**) on *Stypocaulon* and by MOTTIER (**32**) on *Dictyota*. The view that the chromosomes are formed directly from the nucleolus was supported by TANGL (**62**), MEUNIER (**29**), MOLL (**30**), DECAGNY (**10**), HENNEGUY (**19**), VAN WISSELINGH (**67–69**), BERGHS (**3**), KARSTEN (**22**), and TRÖNDLE (**64**) in their studies of *Spirogyra*, by WOLFE (**70**) on *Nemalion*, by LEWIS (**27**) on *Griffithsia*, and by SVEDELIUS (**60**) on *Delesseria*. These investigations differ greatly in regard to exactness and details. In some of these papers views are expressed with adequate illustrations, but often the illustrations and text are quite contradictory, and frequently the figures would afford better support to some other interpretation. In their statements, however, these authors seem to agree that some or all of the chromosomes are organized directly from the material of the nucleolus, which in this way either may be used up partly or even entirely.

A fourth opinion is that the chromosomes arise exclusively from the chromatin network, the nucleolus taking no direct part in their development. *Fucus* illustrates the situation. The plates accompanying the studies on *Fucus* by STRASBURGER (**56**), and by FARMER and WILLIAMS (**15**) show this situation, and more details have been furnished by the present author (**73**). *Polysiphonia* (YAMANOUCHI **71**), *Corallina* (DAVIS **8**, and a forthcoming paper by the author), *Zanardinia* (YAMANOUCHI **76**), as well as *Cutleria* and *Aglaozonia*, present a similar situation.

THE ORIGIN OF BIVALENT CHROMOSOMES

Contrasted with the formation of univalent chromosomes in typical mitosis, the origin of bivalent chromosomes is rather complex. As already described, in the resting nucleus of the zoospore mother cell of *Aglaozonia* the chromatin network is composed of granules and fibrils. While in typical mitosis the network finally

becomes transformed into isolated individual chromosomes, the granules and fibrils being entirely used up in the formation, in the reduction mitosis the granular parts become transformed into fibrils, and consequently during the presynaptic stage there are only thread structures within the nucleus. These chromatin threads, at their beginning irregularly thickened and branched, become much evener, and the transformation continues until long continuous threads are formed, which run freely throughout the cavity. The threads thus formed, from the beginning of their transformation to their completion as continuous structures, have a single nature. Entering the synaptic condition, the single threads then shorten and thicken, and become either eccentrically grouped as a loose tangled mass at one side of the nuclear cavity, or are variously scattered all over the membrane. The threads eventually form loops by repeated folding. The number of loops is 24. Each loop folds together at its bent end so that the bent arms come into contact with each other in the culmination of synapsis. As they emerge from synapsis, there are present 24 bivalent chromosomes, which become detached from the nuclear membrane, moving toward various parts of the nuclear cavity.

The relationship of the chromatin threads in prophase, the loops in synapsis, and the bivalent chromosomes of postsynapsis have been clearly traced. A pair of bivalent chromosomes corresponds to one of the loops in synapsis, the loop being formed by a folding back of the chromatin thread, so that a loop in synapsis should be considered as composed of two sporophytic chromosomes associated end to end. The two elements of the bivalent chromosomes separate from each other at the metaphase of the first reduction division, thus effecting what may be regarded as a qualitative reduction.

The origin and behavior of bivalent chromosomes as described for *Fucus* (**73**) and *Zanardinia* (**76**) agree perfectly in essentials with the present account of *Aglaozonia*. For example, figs. 161, 162, and 172, illustrating looping threads in synapsis and chromosomes in late prophase in the zoospore mother cell of *Aglaozonia*, when compared with figs. 43, 44, and 49 illustrating similar stages of *Fucus* (**73**), demonstrate at once their similarities.

Disregarding many points which may differ in particulars, the case of *Aglaozonia*, in which bivalent chromosomes in seemingly reduced number have originated by the folding back of sporophytic chromosomes united end to end, will agree in essentials with observations made by different authors on various forms, for example, by FARMER and MOORE (**13, 14**), SCHAFFNER (**52**), and MOTTIER (**34**) on *Lilium*, by STRASBURGER (**58**) on *Galtonia*, and by one group of zoologists, such as VON RATH (**37**) on *Gryllotalpa*, RÜCKERT (**41**) on copepods, and MONTGOMERY (**31**) on *Peripatus*.

In general, while the method of forming bivalent chromosomes by the end to end fusion of sporophytic chromosomes or *métasyndèse*, as GRÉGOIRE (**17**) calls it, occurs in *Fucus*, *Zanardinia*, *Aglaozonia*, and other forms, there is also another method by side to side fusion, or *parasyndèse*, in *Polysiphonia* (**71**), *Nephrodium* (**72**), *Osmunda* (**75**), and various other forms, such as *Lilium* (GRÉGOIRE **16**, BERGHS **2**, ALLEN **1**), *Allium* (BERGHS **2**), *Trillium* (GRÉGOIRE **16**), and *Drosera* (ROSENBERG **40**). From these observations it is evident that in the former class there is no duality in the formation of thread structures (*leptotènes*) from the resting nucleus, and therefore in synapsis the two bent arms of a single loop come into close association; and in the latter class, a duality is present at the time of the beginning of the thread structures (*leptotènes*), and the two independent members of the duality come into contact during synapsis. In both classes, each of the two elements of the bivalent chromosome is derived from a single sporophytic chromosome, and the two elements separate in the first division. It seems highly probable that there are two distinct types of arrangement of sporophytic chromosomes at synapsis in plant cells.

POLAR ORGANIZATION

Views on the polar organization of plant cells are conflicting. Some of the algae present clear evidence of such polarity, the best known examples being *Stypocaulon* and *Sphacelaria* (**61**), which have a center in the form of an aster with a centrosome at the side of the resting nucleus of the apical cell. The centrosome is said to divide previous to each mitosis, to establish the poles of the spindle. A similar centrosome with radiations is present in the

tetraspore mother cell of *Dictyota* (**32, 66**). Other algae, such as *Corallina* (**8**), *Fucus* (**15, 56, 73**), *Polysiphonia* (**71**), show highly advanced centrospheres at the poles of the spindle; but investigators claim that in *Corallina* and *Polysiphonia* they appear simultaneously at the two poles during prophase, culminate at metaphase, and disappear at anaphase or telophase; and in *Fucus* one of them appears before the other and they disappear at telophase; only as rare cases they remain recognizable at the side of the resting nucleus. Thus, so far as present knowledge goes, the persistent continuity of polar organization in algae cells has not been demonstrated through successive cell generations.

The subject of polar organization has received especial attention in HARPER'S studies on mildews, especially *Phyllactinia* (**18**). In this form, the "central body" lies within the membrane of the resting nucleus, and it is connected with chromatin strands so as to give polarity to the nucleus. The poles of the spindle are formed by division of the central body. HARPER believes in the permanence of this structure from mitosis to mitosis, and in the persistence of its connection with chromatin.

The studies of recent years on the cells of pteridophytes and spermatophytes have failed to support certain claims for the presence of centrosomes and have indicated that their cells are without visible polar organization. MARQUETTE (**28**) published the view that the presence of polarity in the leaf cell of *Isoetes* is manifested by a large starch-containing body that lies closely pressed against the side of the nucleus. Previous to nuclear division, according to MARQUETTE, the polar structure divides, and during mitosis the structure persists up to telophase, and finally one of them remains at the side of the newly formed daughter nucleus, and a similar constriction division occurs in the structure previous to the next nuclear division. He also found a polar organization of the spore mother cell of *Marsilia*, in the form of aggregated starch grains, conspicuous at the time of synapsis, but disappearing just before the formation of the first spindle; the organization is of very short duration, not continuing throughout the mitosis.

In *Cutleria* and *Aglaozonia*, polar organization is manifested by the appearance of centrosome-like structures with or without

radiations, always only at metaphase, and as a rule completely disappearing at telophase. It may be found that polarity does not depend in all cases upon the presence of permanent protoplasmic structures of recognizable size or upon such morphological differentiation as to rank as organs of the cell. There may possibly be polarity at times without visible protoplasmic organization, but so far as the visible organization of the cell is concerned, there seems to be no permanent polar organization in the cells of *Cutleria* and *Aglaozonia*. The transient polar organization is formed *de novo* at each mitosis in every possible position about the nucleus. The variability of the polar axis of the mitotic figure demonstrates the feature (fig. 13).

Zoospores and gametes of algae invariably present a conspicuous polarity in that their cilia are situated at one end or at a definite point on the side, the point of insertion being devoid of plastids. The most vital problem of zoospore and gamete formation is whether the polar organization of these cells arises *de novo* at the time of development or is handed down from the succession of the cells that are their progenitors. STRASBURGER (**57**), from his studies of the zoospores of *Oedogonium*, *Cladophora*, and *Vaucheria*, decided that the cilia bearing organ, the blepharoplast, arises in the plasma membrane (*Hautschicht*), the nucleus lying in close association at the time of its formation. MOTTIER (**33**) later described a similar origin of the blepharoplast in *Chara*. DAVIS' work on *Derbesia* (**9**) showed that the blepharoplast is developed at the plasma membrane in the form of a ring that has been organized by the side by side union of numerous granules arranged in a circle. The marked polarity is manifested after the appearance of the granules.

The details of the organization of zoospores and gametes of *Cutleria* and *Aglaozonia* have not been given in this account because the subject will be dealt with in a special paper treating of the origin of motile sperms or spores of algae, such as *Fucus*, *Zanardinia*, *Ectocarpus*, and of some green algae, so that a brief account will be sufficient for the present consideration of polarity.

In the zoospore mother cell stage, which is usually reached at the 8-nucleate stage of the zoosporangium, cleavage furrows start

from the periphery and cut into the protoplasm in the form of curved and branching furrows. Finally, the protoplast within the sporangium becomes divided into approximately equal masses, each of which contains a single nucleus. These masses are zoospore primordia, and each develops into a uninucleate zoospore. The nucleus lies first at the center of the zoospore primordium, with plastids lying near the periphery of the cell. The polarity of the cell is clearly established when the nucleus moves toward the peripheral region of the cell, displacing all the plastids in the vicinity, except one which remains near the nucleus. At this time a small granule can be seen lying in the plasma membrane near the nucleus. This granule becomes the blepharoplast, and in a part of the body of the plastid remaining near the nucleus there is later developed a red pigment which makes it look as if the cilia had arisen from the red pigment.

Thus the polarity of the zoospore is manifested only after the organization of the blepharoplast and red pigment spot in the plastid. Again, after its quiescence, the exhibition of polarity is lost until either the segmentation of the nucleus or the elongation of the cell wall begins.

ALTERNATION OF GENERATIONS

Since the classical investigations of HOFMEISTER (**20**), it has been universally recognized that the Archegoniatae are characterized by a definite alternation of generations. In this group there are two regularly alternating generations, one bearing sexual reproductive organs and the other producing spores. In sharp contrast to the unanimous agreement in regard to the existence of an alternation of generations in the Archegoniatae, there is a lively contest of contradictory views as to the alternation of generations in the thallophytes. The thallophytes being a loose assemblage of widely diversified types, and investigations on their life histories being far from numerous enough to permit of any generalization, some still question whether a regular alternation of definitely established generations exists in the group, and if it exists, whether it is to be regarded as homologous or antithetic.

Perhaps the first clear statement of a regular alternation of generations in thallophytes is by SACHS (**42**), who endeavored to bring together the facts known in algae and fungi, and to compare them with alternation in the Archegoniatae. SACHS states that the life cycle of algae and fungi is similar to that of the Archegoniatae, one generation producing sexual organs, and the other forming spores. PRINGSHEIM (**36**) held quite a different view, namely that the alternation of generations in the thallophytes consists in the regular succession of a non-sexual or "neutral" generation with a sexual generation, both generations being of similar structure.

Both these views, one by SACHS, who recognized two distinct generations in thallophytes, and the other by PRINGSHEIM, who regarded the two alternating generations as similar structures, have continued to find followers. VINES (**65**) held the view that most of the thallophytes have no alternation of generations, since both sexual and asexual modes of propagation are directly dependent upon the external conditions, and that an alternation of generations in algae comparable to that in the bryophytes is only found in *Coleochaete* and *Chara*. CELAKOVSKY (**5**), although opposing PRINGSHEIM in his conception of alternation of generations in the Archegoniatae, which he designated as the "antithetic," agreed with him in his conception of alternation in thallophytes, in which the successive generations are alike and which conception he designated as the "homologous." PRINGSHEIM'S conception of the homologous alternation of generations in the Archegoniatae has received its principal support in LANG'S experimental cultures (**26**) of the apogamous development of the sporophytes on prothallia of several pteridophytes. CELAKOVSKY'S conception of alternation of generations in the Archegoniatae was taken up fifteen years later by BOWER (**4**), who has supported this conception by his theory of an interpolated sporophytic generation. BOWER holds that the antithetic alternation originated by the intercalation of a non-sexual generation as a new development between two gametophytic generations. This interpolation of a special sporophyte probably took place, according to BOWER, in the algae-like ancestors of the Archegoniatae as they emerged from an aquatic

life to a land life. Moreover, some of the thallophytes, such as *Coleochaete*, Ascomycetes, and Florideae, he holds show the beginning of an antithetic alternation. STRASBURGER (**54**), summarizing cytological results, advanced the theoretical conception of the periodic reduction of chromosomes in the life cycle in plants, thus establishing the view that the x and $2x$ generations which complete the life cycle of the plant are quite distinct from each other. This view has proved the antithetic character of the two generations from a cytological standpoint.

Since that time, cytological investigations of algae which directly touch the problem of the alternation of generations are those of KLEBS (**23**), WILLIAMS (**66**), WOLFE (**70**), LEWIS (**27**), SVEDELIUS (**60**), and of the author (**71, 73, 74, 76**).

KLEBS conducted experimental cultures of several algae, such as *Vaucheria*, *Oedogonium*, and others. By controlling factors such as light, temperature, moisture, oxygen, and chemical composition of nutritive media, he succeeded in producing any kind of reproduction, either sexual or asexual; in other words, he observed no regular alternation of neutral and sexual generations.

WILLIAMS discovered a reduction of chromosomes during the tetraspore formation in *Dictyota*, and this led him to conclude that the tetrasporic plant of *Dictyota* is a sporophytic generation derived from the fertilized egg.

WOLFE showed for *Nemalion* that the cells of the cystocarp have double the number of chromosomes found in the sexual plant, thus presenting the first cytological evidence that the cystocarp of the red algae is sporophytic in character. He placed the period of chromosome reduction at the time of carpospore formation, basing his conclusion on a count of chromosomes in the mitosis just previous to the formation of the carpospores. However, he did not describe the phenomena characteristic of chromosome reduction, namely, the period of synapsis followed by the two divisions which distribute the chromosomes so as to give a numerical reduction.

After the publication of WILLIAMS' and WOLFE'S work, STRASBURGER expressed his agreement with WILLIAMS' conclusion concerning the alternation of generations in the brown algae, but remarked that the tetraspores of the red algae seemed to be different

from those of the Dictyotaceae, and that the place of the chromosome reduction in the red algae should be sought elsewhere than at the formation of tetraspores because some of the red algae develop no tetraspores, but monospores instead. But immediately after the appearance of this view of STRASBURGER, the author's work on *Polysiphonia* was published. He found that the reduction of chromosomes, instead of taking place at the formation of carpospores as reported by WOLFE, occurred at the development of the tetraspores. Thus in the life cycle of *Polysiphonia*, the sporophytic generation is not only represented by cystocarpic branches, but also extends to the tetrasporic plant that alternates antithetically with the sexual plant.

LEWIS then worked out the cytology of *Griffithsia*, special attention being paid to the problem of the alternation of generations. The place of the reduction of chromosomes is in tetraspore formation as in *Polysiphonia*. He concludes that there is in *Griffithsia* as in *Polysiphonia* an antithetic alternation of generations, the gametophytes being represented by the sexual plants and the sporophytes by the sporogenous cells of the cystocarps. In addition to this, there is a regular succession of tetrasporic individuals and sexual individuals; tetrasporic individuals resemble the gametophytes in morphological differentiation and the sporophytes in number of chromosomes. He regards the tetrasporic and sexual plants as presenting homologous alternation.

SVEDELIUS studied the alternation of generations in *Delesseria*. Although his work does not cover the whole life cycle of this type, the cytological studies being made only in the development of tetraspores and vegetative mitosis in both tetrasporic and female plants, yet by comparing his work with that on *Nemalion*, *Polysiphonia*, and *Griffithsia*, he has come to the conclusion that there is an alternation of generations in *Delesseria* as in *Polysiphonia*.

The existence of an alternation of generations in the thallophytes, though somewhat obscure in the green algae on account of insufficient investigations, has been clearly proved by the cytological studies on *Fucus* and *Dictyota* among the brown algae, and on *Nemalion*, *Polysiphonia*, *Griffithsia*, and *Delesseria* among the red algae. Let us now turn to the situation in *Cutleria*.

Since FALKENBERG (12) first suggested that *Cutleria* and *Aglaozonia* may represent the two phases of the life cycle of a single species (*Cutleria*), many workers have tried to secure *Aglaozonia* plants from the cultures of fertilized gametes of *Cutleria*. FALKENBERG and REINKE were the only two who succeeded in producing the form *Falkenbergiana*, an *Aglaozonia* form. The rest of the investigators succeeded in producing either the form *Falkenbergiana* or the form *Churchiana* from unfertilized gametes. Among later workers, SAUVAGEAU, by carrying on his cultures for years, succeeded in getting *Aglaozonia* or *Cutleria* from unfertilized gametes of *Cutleria adspersa*. The conclusion drawn from this result naturally was that the alternation of generations is not necessary, but rather, as it might be called, facultative. OLTMANNS and STRASBURGER have agreed with this view of SAUVAGEAU. The so-called polymorphic character of *Cutleria*, however, needs analytical consideration. The results of the author's investigation are as follows:

The investigation of *Cutleria* plants bearing gametangia showed that the nucleus has 24 chromosomes in both the vegetative and germ cells. The number is doubled at fertilization by the union of the sexual nuclei. The *Cutleria* plant is therefore a gametophyte whose chromosome number is 24. As all now agree, the fertilized gamete or egg with its fusion nucleus should represent the $2x$-generation, and so the fertilized gamete of *Cutleria* is the beginning of the $2x$-generation. The studies of the germination of the fertilized gamete have shown that the $2x$ condition continues in further development. The sporeling developed into a structure unlike the young filamentous form of the parent *Cutleria* as found in nature, but composed of a small upright column and a proportionally large basal disk expansion which became later the dominating region of the further development. Later this expansion develops the zonal structure of *Aglaozonia* as found in nature, and not only resembles *Aglaozonia* in outer morphology, but also in the nuclear conditions, the expansion in cultures and *Aglaozonia* in nature both having 48 chromosomes. *Aglaozonia* in nature produces zoospores, during whose formation 48 chromosomes are reduced to 24, and the zoospores contain 24 chromosomes. The

zoospore with the haploid number germinates with no fusion. The product of the zoosporeling is a filamentous individual like young *Cutleria*, and never produces the zonal flattened form of the parent *Aglaozonia*.

The condition in cultures is very different from the environment in nature. In nature the gametes and zoospores are set free at a depth of 1–5 meters and in cultures they are discharged and kept in sea-water at a depth less than 15–20 cm. Besides, the intensity of light, water-pressure, temperature, and motion of water are also different in these two different environments, and yet the sporelings of the fertilized gametes developed into the flattened disk like young *Aglaozonia* and those of the zoospores grow into filamentous plants like young *Cutleria*. That the potentialities of those two kinds of sporelings in forming invariably the particular individuals different from the parent forms as in nature, even under environmental conditions so different from what is found in nature, and that the potentialities of the two different sporelings have given rise to the particular different individuals, even when they were kept in similar cultures, show that the potential characters of their germ plasm has dominated over the influence of environmental conditions; this dominancy of the innate character over the environmental influence is fundamentally different from the experiments of KLEBS on certain green algae (**23**). Although the two kinds of sporelings from fertilized gametes and zoospores in the cultures have not been kept growing to the stage of reproduction, yet it seems safe enough to infer that the disklike expansion developed from the sporelings of the fertilized gamete will be identical with *Aglaozonia* as found in nature, and the filamentous structures of the zoosporelings will be *Cutleria*. Thus *Cutleria* plants with zoospores represent a gametophytic generation, and *Aglaozonia* plants with fertilized gametes the sporophytic generation. These two generations alternate in the life history of *Cutleria*. The two generations, from the above observations of the cell organization, are fundamentally different and could not be regarded as an example of polymorphism in the sense of OLTMANNS (**35**).

The observations on the sporelings of the unfertilized gametes and studies of their cell organization undoubtedly show that the

female gametes of *Cutleria* are capable of developing into the flattened disk like *Aglaozonia* in nature. Though at first their external morphology presents irregular deviations from forms in nature, the nuclear divisions are perfectly normal. The culture of the sporelings was not continued up to production of reproductive organs, and consequently the discussion cannot be carried on any further. This apogamy may indeed be a reversion to the ancestral type of asexual spores which certainly existed before the appearance of sexuality in the gametophytic generation, but when sexuality is once established, the fusion of gametes and thereby the sporophytic generation is interpolated as a secondary structure in which the reduction of chromosomes occurs.

Summary

The nuclear conditions in the life history of *Cutleria multifida* may be summarized as follows:

1. The nucleus of both male and female plants contains 24 chromosomes, and the male and female gametes contain the same number.

2. In the union of gametes the number is doubled, and 48 chromosomes appear in the sporelings, which develop into the *Aglaozonia* form of *Cutleria*. Therefore, the individual bearing the name of *Cutleria multifida* represents the gametophytic phase of the species, 24 being the gametophytic number of chromosomes; and the *Aglaozonia* form of *Cutleria* represents the sporophytic phase, 48 being the sporophytic number.

3. *Aglaozonia reptans* contains 48 chromosomes, and the number is reduced in zoospore formation, the zoospore containing 24 chromosomes. The zoospore with the reduced number of chromosomes germinates without conjugation. The individual grown from the germinating zoospore presents a striking similarity to the young form of *Cutleria* in nature and contains 24 chromosomes, the same number as the latter. Therefore it is evident that the individual bearing the name of *Aglaozonia reptans* represents the sporophytic phase of the species, 48 being the sporophytic number of chromosomes, and that the gametophytic phase is represented

by the individual grown from the zoospore and resembling the young form of *Cutleria* in nature. It is certain that *Aglaozonia reptans* as it occurs in nature is identical with the *Aglaozonia* form of *Cutleria multifida* as developed in cultures and now determined to be the sporophytic phase of the species.

4. Therefore, *Cutleria multifida* and *Aglaozonia reptans* represent respectively gametophytic and sporophytic generations of a single species, the two generations alternating in the life history of *Cutleria*.

5. The female gamete of *Cutleria* may germinate apogamously. There is no irregularity in the mitotic process, 24 chromosomes being invariably present. The individual produced, in its early development differs somewhat from the product of the fertilized gamete, but the fate of the apogamous individual was not determined.

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EXPLANATION OF PLATES XXVI–XXXV

All figures were drawn with the aid of a camera lucida under the Zeiss apochromatic objective 1.5 mm. N.A. 130, in combination with compensating ocular 12; except figs. 200–202, which were drawn with compensating ocular 18; figs. 8, 9, 14, drawn with compensating ocular 8; and figs. 1–7, 12, 13, 16, 17, 53, 144–150, drawn with ocular 4; and figs. 10, 11, 15, which were drawn under Zeiss apochromatic objective 16 mm. combined with compensating ocular 12. The figures are reduced to one-half the original size. Figs. 1–15 are in the text.

PLATE XXVI

The formation of the male gametangium of Cutleria multifida

FIG. 16.—Portion of the thallus of a male plant, showing a single layer of superficial cells and the larger cells below.

FIG. 17.—Portion of the thallus of a male plant, where 4 superficial cells have grown into papillae, the male gametangium initials.

FIG. 18.—Male gametangium initial: nucleus in resting condition.

FIG. 19.—Prophase of nucleus: 24 chromosomes and a nucleolus present.

FIG. 20.—Metaphase: the nuclear cavity in this stage strikingly diminished.

FIG. 21.—A filament with two male gametangia: nucleus in the young gametangium initial at metaphase.

FIG. 22.—Anaphase that follows the metaphase of fig. 20.

FIG. 23.—Nucleus already divided and each daughter nucleus now in prophase; 24 chromosomes present in each.

FIG. 24.—Nucleus in the lower cell in advanced prophase, while the nucleus in the upper cell is still in early prophase.

FIG. 25.—Similar stage to fig. 24, excepting the presence of centrosome-like structures at the poles.

FIG. 26.—Nucleus in the lower cell in anaphase; nucleus in the upper cell in resting condition.

FIG. 27.—Metaphase of the nucleus in the upper cell of 2-celled stage; the lower cell is not drawn.

FIG. 28.—Late metaphase of the nucleus in the upper cell; nucleus in the lower cell in resting condition.

FIG. 29.—Telophase of nucleus of the upper cell; a new cell wall is being laid down between two daughter nuclei.

FIG. 30.—Male gametangium of 3 cells: the nuclei in the upper two cells are in resting condition; the nucleus in the basal cell in prophase, showing 24 chromosomes and a nucleolus.

FIG. 31.—Male gametangium of 3 cells: the nucleus in the terminal cell is in metaphase; centrosome-like structures at the poles of the spindle.

FIG. 32.—Male gametangium of 3 cells: the nucleus in the terminal cell in metaphase, with centrosome-like structures at the poles; the nucleus in the middle cell in anaphase, and that of the basal cell in resting stage.

FIG. 33.—Male gametangium of 4 cells: the nucleus in the terminal cell is in metaphase; that of the middle cell in prophase, showing 24 chromosomes.

FIG. 34.—Male gametangium of 4 cells: two nuclei are in prophase; 24 chromosomes are clearly present; one in anaphase and the other in resting condition.

FIGS. 35, 36.—Mitotic figures of the nucleus in a vegetative filament: fig. 35, anaphase; fig. 36, prophase, showing 24 chromosomes.

FIGS. 37, 38.—Cross-section of a male gametangium of 5 cells: fig. 37, metaphase of the mitosis which divides the filament into two rows of cells; fig. 38, prophase of the same, showing 24 chromosomes.

FIG. 39.—Tip of a vegetative filament, showing stages in the formation of male gametangia; the male gametangia have arisen from the third, fourth, sixth, and seventh cells; four nuclei in the three young gametangia are in prophase; 24 chromosomes can be counted in each.

FIG. 40.—Portion of a male gametangium of 2 rows of cells: one nucleus in metaphase, one in prophase showing 24 chromosomes, and three others in the resting condition.

FIG. 41.—Portion of a more advanced male gametangium: four nuclei in prophase, clearly showing the 24 chromosomes.

FIG. 42.—Cross-section of a male gametangium at about the same stage as in fig. 41; one nucleus is in prophase; 24 chromosomes present.

FIG. 43.—Portion of a male gametangium at about the same stage as in fig. 41; two nuclei are in anaphase.

FIG. 44.—Cross-section of a male gametangium at about the same stage as in fig. 43: two nuclei in prophase of the mitosis which divides the filament into a structure with four rows of cells.

FIG. 45.—Portion of a male gametangium consisting of 4 rows of cells: one nucleus is in anaphase.

FIG. 46.—Portion of a male gametangium at about the same stage as in fig. 45: one nucleus is in prophase, showing clearly 24 chromosomes.

FIGS. 47, 48.—Portion of a male gametangium at a more advanced stage: one nucleus in fig. 47 in prophase, showing 24 chromosomes; one nucleus both in figs. 47 and 48 in metaphase; and two nuclei in fig. 48 in anaphase.

FIG. 49.—Portion of a male gametangium, showing the last division of nuclei; one nucleus is in prophase and the other in metaphase.

FIG. 50.—Cross-section of a male gametangium at about the same stage as in fig. 49; one nucleus is in prophase, two others in metaphase of the mitosis which divides the filament into a structure of 8 rows of cells.

FIG. 51.—Cross-section of a mature male gametangium: nuclei are in resting condition.

FIG. 52.—Cross-section of a mature male gametangium, showing the plastids that are associated with the red pigment.

PLATE XXVII

The formation of the female gametangium of Cutleria multifida

FIG. 53.—Portion of thallus of a female plant, showing a single layer of superficial cells and the larger cells below; one of the superficial cells has increased in size, and will be the female gametangium later.

FIG. 54.—One of the superficial cells becomes still larger in size: nucleus is in prophase; 24 chromosomes and a nucleolus are present.

FIG. 55.—Nucleus in metaphase; centrosome-like structures at the poles of spindle.

FIG. 56.—Anaphase.

FIG. 57.—Later telophase: cell wall is being laid down between the newly formed daughter nuclei.

FIG. 58.—Female gametangium of 2 cells.

FIG. 59.—Nucleus of the upper cell in prophase; nucleus of the basal cell in resting condition.

FIG. 60.—Nucleus of upper cell in metaphase.

FIG. 61.—Nucleus of upper cell in anaphase.

FIG. 62.—Late telophase of nucleus in upper cell.

FIG. 63.—Female gametangium consisting of 2 cells: nucleus of basal cell in metaphase.

FIG. 64.—Nucleus in basal cell in anaphase.

FIG. 65.—Female gametangium of 3 cells: nucleus of basal cell in prophase; 24 chromosomes and a nucleolus are present.

FIG. 66.—Nucleus of terminal cell in prophase, showing 24 chromosomes; nucleus of basal cell in metaphase.

FIG. 67.—Nucleus of terminal cell in metaphase.

FIG. 68.—Nucleus of terminal cell in anaphase.

FIG. 69.—Nucleus of middle cell in prophase.

FIG. 70.—Nucleus of middle cell in early anaphase.

FIG. 71.—Cross-section of a female gametangium of 2 cells: nucleus in anaphase viewed from the pole, clearly showing 24 chromosomes.

FIG. 72.—Cross-section of a female gametangium of 5 cells: nucleus in metaphase of the mitosis which divides the gametangium into a structure composed of 2 rows of cells.

PLATE XXVIII

The formation of the female gametangium of Cutleria multifida (continued)

FIG. 73.—Cross-section of a female gametangium of 8 cells in two rows: one nucleus in late prophase, showing 24 chromosomes.

FIG. 74.—Portion of a female gametangium of 8 cells in two rows: one nucleus in late prophase, polar view of which is shown in the previous figure; nucleus in basal cell in early prophase.

FIG. 75.—Portion of a female gametangium of 7 cells: one nucleus is in late prophase, showing 24 chromosomes, which will result in two cells arranged side by side in the direction perpendicular to the plane of the paper.

FIG. 76.—Portion of a female gametangium of 8 cells: one nucleus in anaphase.

FIG. 77.—Portion of a female gametangium of 8 cells: one nucleus in late anaphase.

FIG. 78.—Cross-section of a female gametangium of 10 cells: one nucleus in metaphase of the division which divides the gametangium into a structure of three rows of cells.

FIG. 79.—Portion of a female gametangium of 10 cells: one nucleus in metaphase.

FIGS. 80, 81.—Portion of a female gametangium of 10 cells: one nucleus in anaphase in both figures.

FIG. 82.—Portion of a female gametangium of 10 cells: one nucleus is in metaphase and two others have already divided.

FIG. 83.—Portion of a female gametangium of 10 cells: one nucleus in prophase, showing 24 chromosomes, one nucleus in late anaphase and the other two have already divided.

FIG. 84.—Portion of a female gametangium of 10 cells: one nucleus in early metaphase viewed from the pole, showing 24 chromosomes.

FIG. 85.—Portion of a female gametangium of 12 cells: one nucleus in anaphase and the other two have already divided.

FIG. 86.—Portion of a female gametangium of 12 cells: one nucleus in early metaphase, viewed from the pole, showing 24 chromosomes; the other nucleus in metaphase in lateral view.

FIG. 87.—Portion of a female gametangium of 15 cells: one nucleus in prophase.

FIG. 87*a*.—The nucleus in prophase in the previous figure under higher magnification: 24 chromosomes present.

FIGS. 88, 88*a*.—Portion of a female gametangium of 18 cells: one nucleus in anaphase, which is shown under higher magnification in fig. 88*a*.

FIG. 89.—Cross-section of mature female gametangium in 4 tiers.

FIG. 90.—Cross-section of mature female gametangium in 8 tiers.

FIG. 91.—Two cells of a mature female gametangium: the plastids and dense cytoplasm are thick along the inner wall; nuclei in resting condition.

FIG. 92.—One cell of a mature female gametangium: plastids and cytoplasm are thick toward the outer wall; nucleus in resting condition.

FIG. 93.—A female gametangium entirely emptied after the escape of female gametes.

PLATE XXIX

The union of gametes and germination of the fertilized female gamete

FIG. 94.—Two male gametes which have stopped the swimming movement; cilia are withdrawn, nuclear membranes are scarcely visible, and the reticulum shows 24 chromosomes.

FIG. 95.—Union of male and female gametes: nucleus of the male gamete shows 24 chromosomes and that of the female gamete is in the resting condition; no cell membrane is recognizable around the gametes.

FIG. 96.—Cytoplasm of male gamete is entirely fused with that of female gamete and the whole body of the united gametes has about assumed the spherical form; cell membrane has appeared; male nucleus still shows 24 chromosomes.

FIG. 97.—Male nucleus has advanced toward the female nucleus.

FIG. 98.—Male nucleus has moved nearer toward the female nucleus.

FIG. 99.—Male nucleus is attached to the female nucleus.

FIG. 100.—Male nucleus, showing 24 chromosomes, and female nucleus in resting condition.

FIG. 101.—Male nucleus very closely applied to the female nucleus; 24 chromosomes of the male nucleus still recognizable; a part of the cell wall of the sporeling has thickened.

FIG. 102.—Part of the male nucleus, evidently consisting exclusively of chromosomes, has become submerged in the female nucleus, which is in the resting condition.

FIG. 103.—Male nucleus has completely entered into the female nucleus; dense chromatin granules are to be seen at the part of female nucleus where the male nucleus has entered.

FIG. 104.—Fusion nucleus: network contains a number of chromatin granules that show no distinction between those derived from the male and female nuclei.

FIG. 105.—Fusion nucleus is in the resting condition.

FIG. 106.—Prophase: 48 chromosomes and a nucleolus are present; the chromosomes are apparently alike both in form and size; the sporeling shows an elongation at a point where the cell wall is thickened.

FIG. 107.—Metaphase: thickening of cell wall is present, though the elongation of the sporeling has not yet begun.

FIG. 108.—Fusion nucleus in very early prophase: characteristic elongation of the sporeling and thickening of the corresponding cell wall at that part is remarkable.

FIG. 109.—Portion of the elongated part of a sporeling with a resting nucleus.

FIG. 110.—Cross-section of the elongated portion of a sporeling at the same stage as the previous figure; fusion nucleus in prophase; 48 chromosomes are present.

FIG. 111, *a*, *b*.—Two sections of a sporeling: nucleus in prophase, showing 48 chromosomes; elongation and correponding thickening of the cell wall are evident.

FIG. 112.—Metaphase: Elongation of the sporeling and thickening of the cell wall at the point of the elongation are marked; axis of the figure is in the direction of the elongation.

FIG. 113.—Cross-section of a sporeling perpendicular to the axis of elongation; nucleus in late metaphase.

FIG. 114.—Cross-section of a sporeling at about same stage as in fig. 112; nucleus in metaphase is seen from the pole; 48 chromosomes are present.

FIG. 115.—Sporeling in 2-celled stage: two nuclei in resting condition.

FIG. 116.—Sporeling in 2-celled stage: nucleus in terminal cell in prophase, and that of basal cell in resting condition.

FIG. 117.—Sporeling in 2-celled stage: nucleus in terminal cell very small and in resting condition, while that of basal cell shows very early prophase.

FIG. 118.—Cross-section through a basal cell of a sporeling in 2-celled stage: nucleus is in late prophase; 48 chromosomes present.

FIG. 119.—Sporeling in 2-celled stage: nucleus in terminal cell in early prophase, and that of basal cell in resting condition.

FIG. 120.—Sporeling in 2-celled stage: nucleus in terminal cell in prophase, showing 48 chromosomes.

FIG. 121.—Sporeling in 3-celled stage: nucleus in basal cell in prophase, showing 48 chromosomes.

FIG. 122.—Sporeling in 3-celled stage: nucleus in basal cell in metaphase.

FIG. 123.—Sporeling in 3-celled stage: all the nuclei in prophase, showing 48 chromosomes.

PLATE XXX

The germination of the unfertilized female gamete

FIG. 124.—A female gamete in the resting condition: cell wall does not seem to be developed excepting at the point where a slight elongation is noticeable.

FIG. 125.—Cell wall is now recognizable, especially at the elongated point; nucleus in resting condition.

FIG. 126.—Nucleus with 24 chromosomes is prophase.

FIG. 127.—Nucleus in metaphase: contour of sporeling almost spherical.

FIG. 128.—Polar view of same stage as in previous figure: 24 chromosomes.

FIG. 129.—Polar view of metaphase showing 24 chromosomes: characteristic elongation and the thickened cell wall of the elongated part are recognizable.

FIG. 130.—Metaphase of same stage as in previous figure: axis of the figure is perpendicular to that of the previous one.

FIG. 131.—Anaphase.

FIG. 132.—Metaphase of the similar stage as in figure 130, but axis of the figure is perpendicular to that.

FIG. 133.—Anaphase.

FIG. 134.—Late telophase: elongation of the sporeling is remarkable.

FIG. 135.—Sporeling of 2-celled stage: nuclei in resting condition.

FIG. 136.—Sporeling of 2-celled stage: nucleus of terminal cell in prophase; 24 chromosomes present.

FIG. 137.—Sporeling of 2-celled stage: nucleus of terminal cell in metaphase viewed from pole; nucleus of basal cell in prophase; 24 chromosomes present.

FIG. 138.—Sporeling of 2-celled stage: nucleus of terminal cell in prophase; form of the chromosomes is rather long.

FIG. 139.—Sporeling of 2-celled stage: nucleus in basal cell in anaphase.

FIG. 140.—Sporeling of 2-celled stage: nucleus in terminal cell in late telophase and that of basal cell in metaphase, showing 24 chromosomes in polar view.

FIG. 141.—Sporeling in 3-celled stage: nucleus of basal cell in prophase, showing 24 chromosomes.

FIG. 142.—Sporeling in 3-celled stage: nucleus of middle cell in prophase, showing 24 chromosomes.

FIG. 143.—Sporeling in 3-celled stage: nucleus of basal cell in metaphase.

FIG. 144.—Sporeling of 12-celled stage.

FIG. 145.—Sporeling of 13-celled stage.

FIG. 146.—Sporeling of 22-celled stage.

PLATE XXXI

The formation of the zoosporangium of Aglaozonia reptans

FIG. 147.—Portion of a young thallus, showing a single layer of superficial cells and the larger cells below.

FIG. 148.—Portion of a young thallus, showing a single layer of superficial cells, hypodermal cells, and the larger cells below.

FIG. 149.—Portion of thallus in more advanced stage.

FIG. 150.—Portion of thallus in still more advanced stage: superficial cells have grown in size and will be zoosporangia or zoospore mother cells.

FIG. 151.—Young zoospore mother cell and stalk cell.

FIG. 152.—Zoospore mother cell of characteristic club-shape; nucleus in resting condition.

FIG. 153.—Resting nucleus slightly increased in size.

FIG. 154.—Resting nucleus with radiations at one pole.

FIG. 155.—Section of a mother cell cut obliquely: resting nucleus with radiations at two poles.

FIG. 156.—Nucleus in very early prophase, situated at one side, with a centrosome-like structure but no radiations.

FIG. 157.—Nucleus situated at the upper part of the mother cell with two centrosome-like structures and radiations.

FIG. 158.—Nucleus situated at the upper part with a centrosome-like structure and radiations.

FIG. 159.—Nucleus situated at the middle part with no radiations.

PLATE XXXII

The formation of the zoosporangium of Aglaozonia reptans (continued)

FIG. 160.—Nucleus of a zoospore mother cell in prophase, chromatin network irregularly traversing the nuclear cavity.

FIGS. 161–168.—Nucleus in synapsis.

FIG. 161.—Chromatin threads have begun to be arranged in form of loops which become attached by their ends to a part of the nuclear membrane.

FIG. 162.—Formation of loops is further advanced.

FIG. 163.—Cross-section of a mother cell; attachment of loops is at the side.

FIG. 164.—Attachment of loops to the nuclear membrane is all the way around.

FIG. 165.—Some of the loops are quite shortened and thickened, and yet some others are left behind and can be recognized running across the cavity.

FIG. 166.—Section near the base of crowded loops in contact with the membrane, showing 48 or more isolated cut sections of the loops.

FIG. 167.—Loops have shortened and thickened.

FIG. 168.—Nucleus emerging from synapsis: two pairs of chromatin loops are already in the form of chromosomes.

FIG. 169.—Majority of the two arms of each of these loops are going to form paired arms of bivalent chromosomes.

FIG. 170.—Diakinesis stage: 24 bivalent chromosomes are present; no polar radiations.

FIG. 171.—Spindle with two poles has just formed.

FIG. 172.—Metaphase.

FIG. 173.—Polar view of the metaphase, showing 24 bivalent chromosomes at the equatorial plate.

PLATE XXXIII

The formation of the zoosporangium of Aglaozonia reptans (continued)

As the stage advances, gradual increase of the thickening of the cell wall at the tip of the mother cell is noticeable.

FIG. 174.—Late metaphase.

FIG. 175.—Anaphase: 24 chromosomes at each pole.

FIG. 176.—Anaphase, side view.

FIG. 177.—Anaphase, further advanced.

FIG. 178.—Telophase.

FIG. 179.—Later telophase: two daughter nuclei in resting condition.

FIG. 180.—Two daughter nuclei increased in size: each nucleus has radiations at the poles.

FIG. 181.—Upper nucleus has grown considerably larger than the lower one.

FIG. 182.—Two nuclei are in contact.

FIG. 183.—Upper nucleus is in prophase; lower one still in resting condition.

FIG. 184.—Two nuclei simultaneously in metaphase.

FIG. 185.—Anaphase.

FIG. 186.—Late anaphase: a group of chromosomes at one pole of the upper nucleus is not indicated in this figure.

PLATE XXXIV

The formation of the zoosporangium of Aglaozonia reptans (continued)

FIG. 187.—Telophase of the second division in the mother cell.

FIG. 188.—Late telophase.

FIG. 189.—Metaphase of the third division.

FIG. 190.—Telophase of the same: 8 nuclei present.

FIGS. 191–193.—Zoospore mother cells drawn from unstained preparations.

FIG. 191.—Nucleus in prophase: numerous granules of various sizes are recognizable; globular structures of larger size are plastids.

FIG. 192.—Four-nucleate stage: numerous granules still visible; plastids have increased in number.

FIG. 193.—Eight-nucleate stage: plastids have much increased in number and the thickness of the cell wall at the top of the mother cell is noticeable.

FIG. 194.—Cross-section of a mother cell at about same stage as in fig. 190; plastids mostly arranged near the cell membrane.

FIG. 195.—Portion of a mother cell near maturity: thickness of the cell wall at the top of the mother cell has increased; plastids moving toward the nuclei and surrounding them.

FIG. 196.—Later stage: plastids are around the nuclei.

FIG. 197.—Portion of a mother cell: cytoplasm has become detached from the cell wall and cleavage furrows have appeared, so that general outlines of individual zoospores are established.

FIGS. 198, 199.—Portion of a mother cell containing zoospores.

FIG. 200.—Portion of cell wall at the tip of a mother cell after maturity: the cell wall in this part is considerably thickened and swollen.

FIG. 201.—Later stage: the cell wall at the tip of the mother cell has disintegrated into two lamellae.

FIG. 202.—Further advanced stage approaching the discharge of zoospores: disintegration has still progressed and broken the cell wall into three lamellae.

PLATE XXXV

The germination of the zoospore of Aglaozonia reptans

FIG. 203.—Zoospore 2 hours after becoming quiescent: cell wall has just developed; resting nucleus with a centrosome-like structure and radiations.

FIG. 204.—Zoospore 20 hours after becoming quiescent: nuclear condition is about similar to fig. 203.

FIG. 205.—Zoospore 24 hours after becoming quiescent: no radiations visible.

FIGS. 206–208.—Drawn from material fixed 24 hours after becoming quiescent.

FIG. 206.—Resting nucleus with radiations: elongation of the sporeling and thickening of cell wall at the elongated part is noticeable.

FIG. 207.—About the same stage as in the previous figure.

FIG. 208.—Early prophase.

FIG. 209.—Prophase: 24 chromosomes clearly present.

FIG. 210.—Cross-section through the elongated part of a sporeling: nucleus in prophase, showing 24 chromosomes and a nucleolus.

FIG. 211.—Metaphase: general contour of the sporeling is spherical.

FIG. 212.—Polar view of the metaphase; 24 chromosomes clearly in view.

FIG. 213.—Metaphase: the sporeling has elongated.

FIG. 214.—Metaphase viewed from the pole: the sporeling has elongated at two points.

FIG. 215.—Anaphase.

FIG. 216.—Telophase.

FIG. 217.—Sporeling of 2 cells: nucleus of the basal cell is in prophase; 24 chromosomes visible.

FIG. 218.—Sporeling of 2 cells: nucleus in metaphase.

FIG. 219.—Sporeling of 2 cells: nucleus of terminal cell in early prophase; 24 chromosomes present.

FIG. 220.—Nucleus of terminal cell in prophase.

FIG. 221.—Nucleus of terminal cell in metaphase viewed from pole.

FIG. 222.—Two nuclei simultaneously in prophase; 24 chromosomes present.

FIG. 223.—Sporeling of 3 cells.

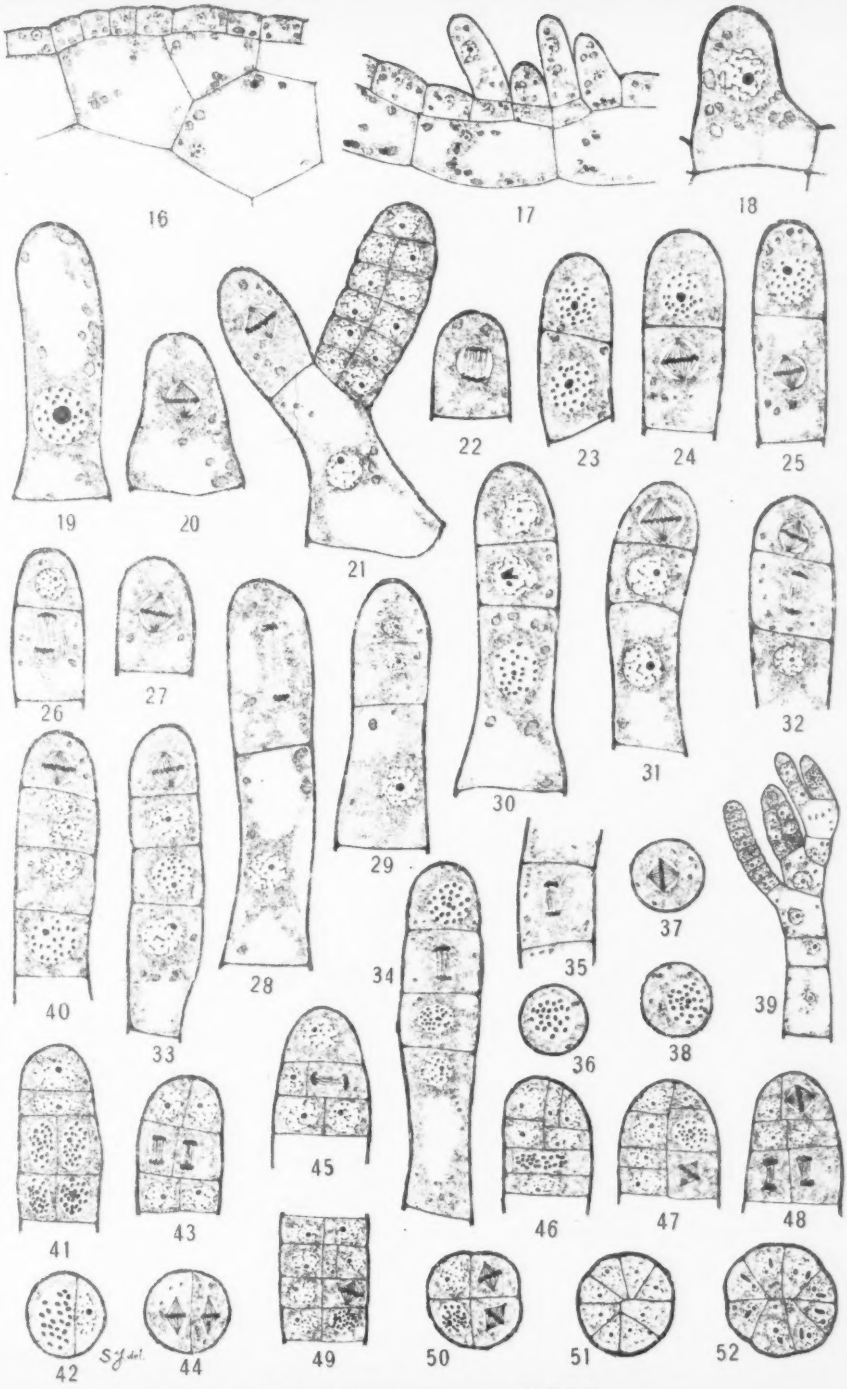
FIG. 224.—Sporeling of 3 cells: nucleus in middle cell in prophase; 24 chromosomes present.

FIG. 225.—Sporeling of 3 cells: nucleus in basal cell in prophase; 24 chromosomes present.

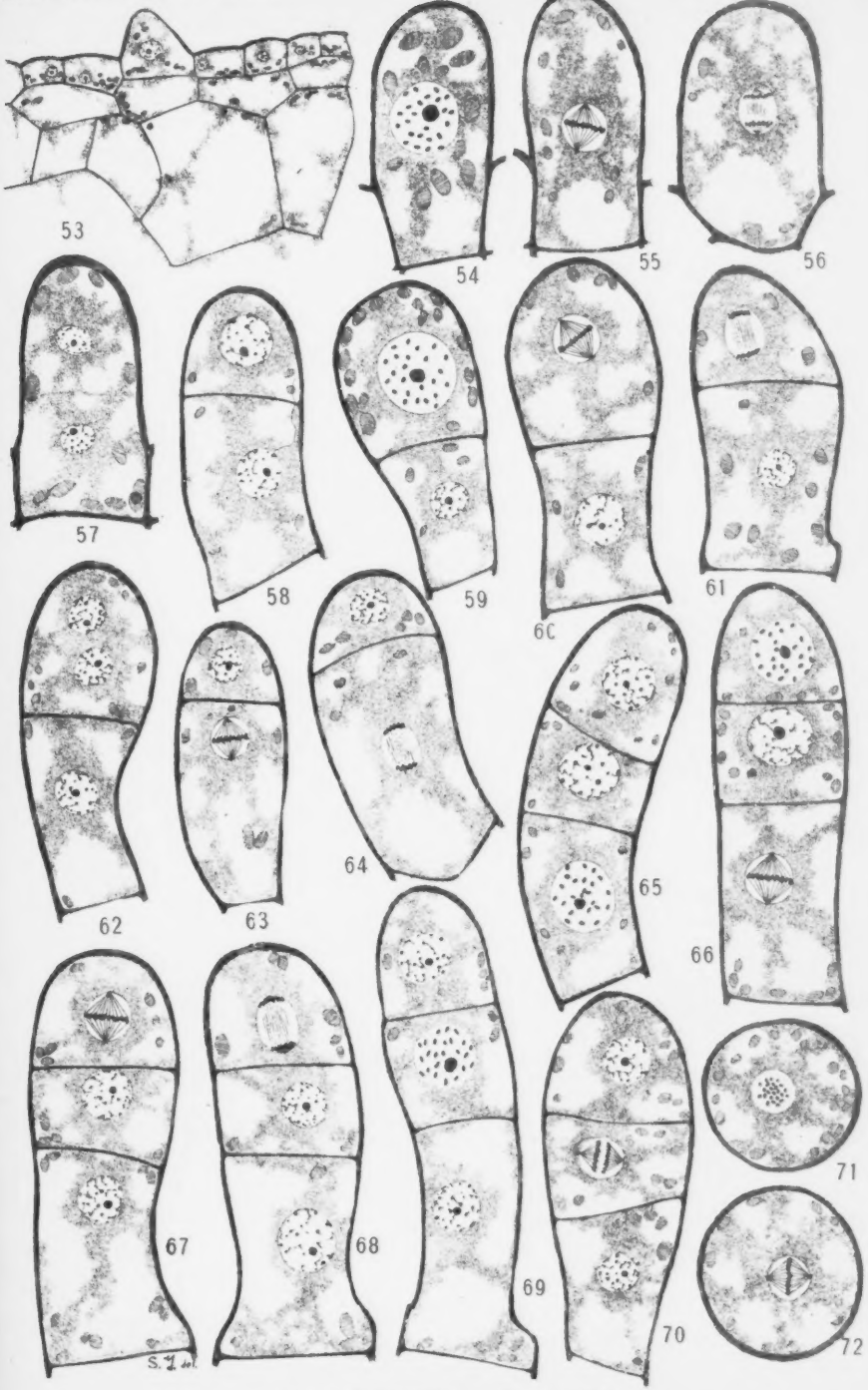
FIG. 226.—Sporeling of 4 cells.

FIG. 227.—Sporeling of 4 cells: nuclei in lower cells in metaphase.

FIG. 228.—Sporeling of 4 cells: two upper cells lie side by side in the direction perpendicular to the axis of the sporeling.



YAMANOUCHI on CUTLERIA



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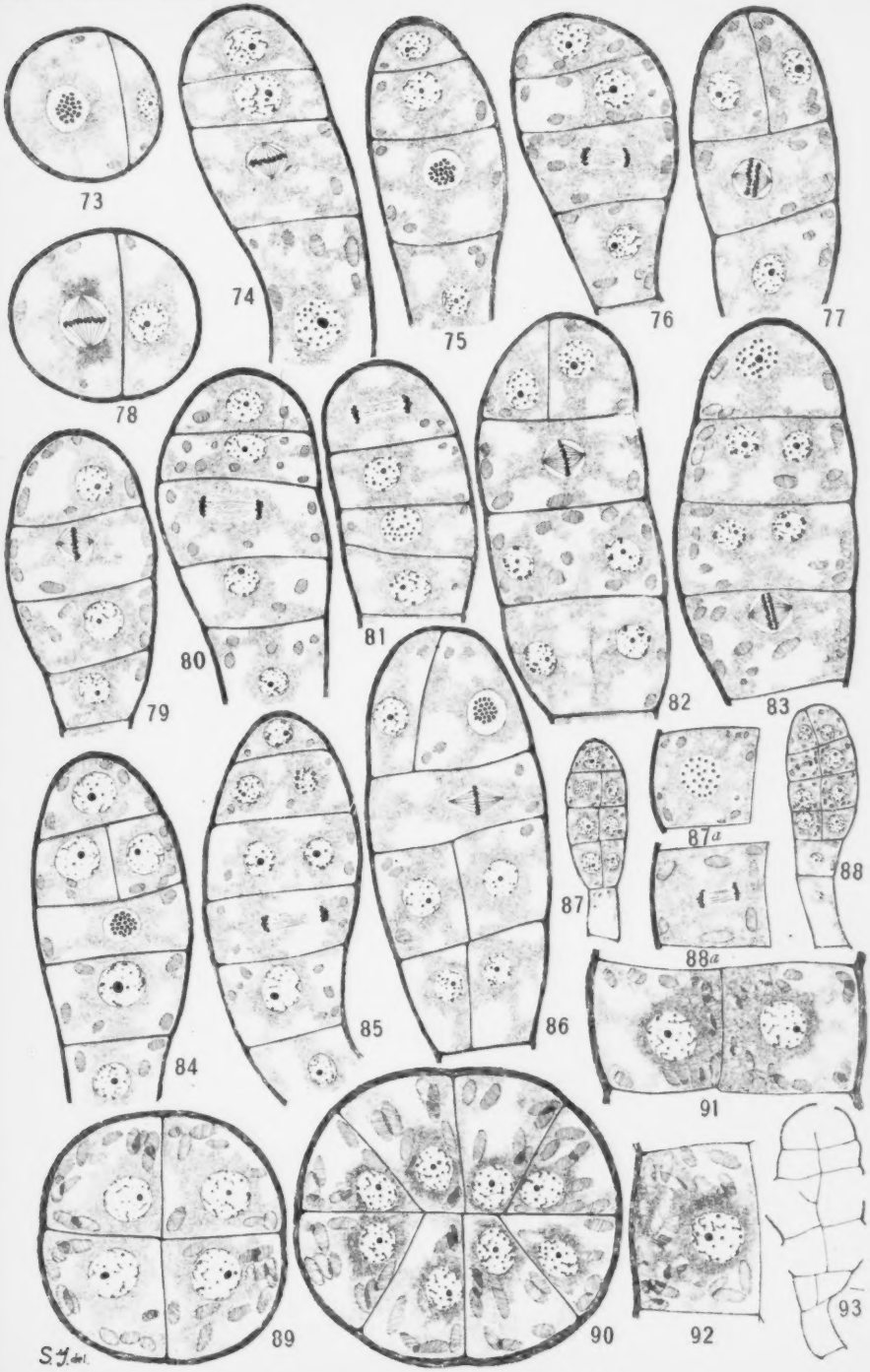

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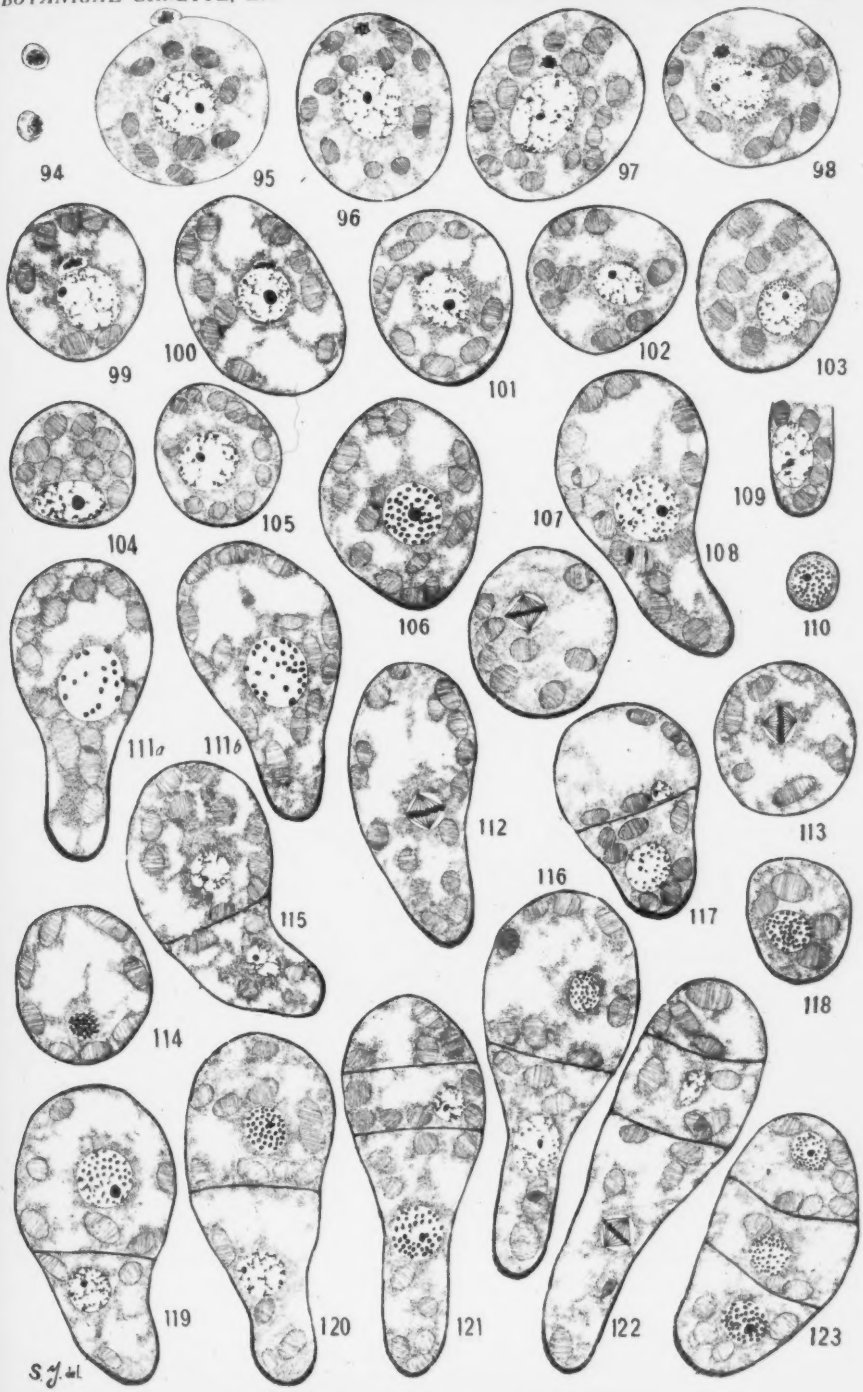

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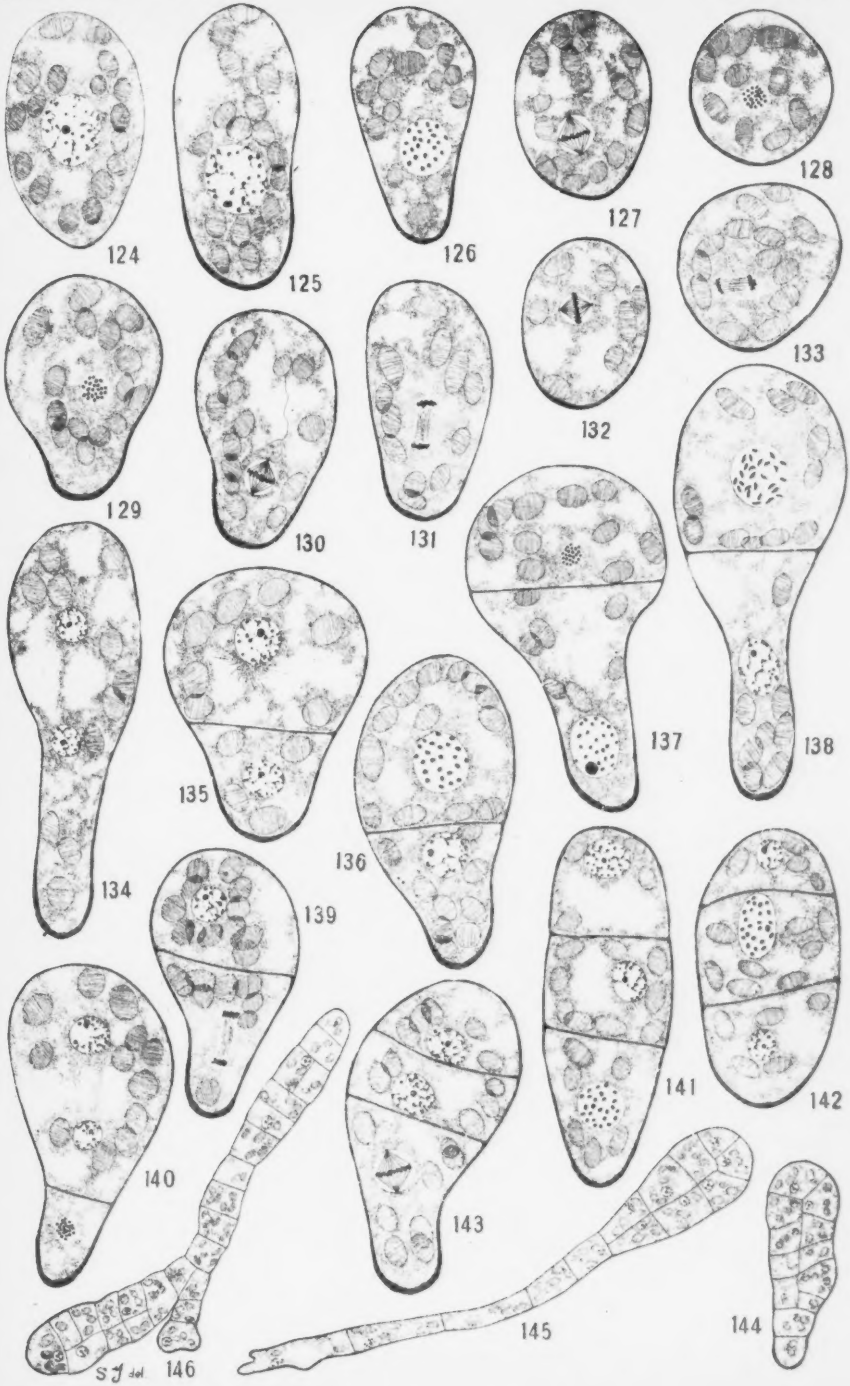

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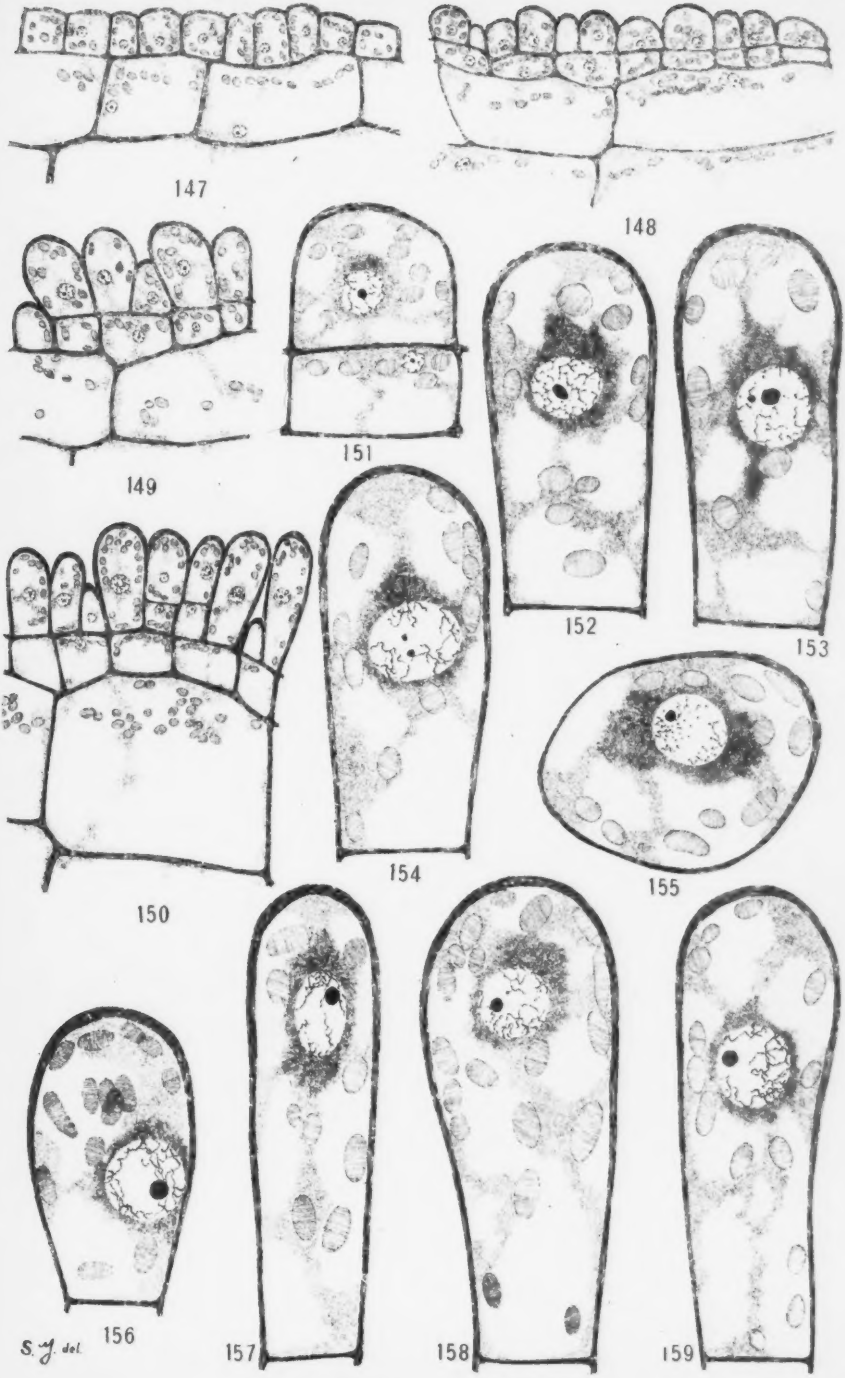

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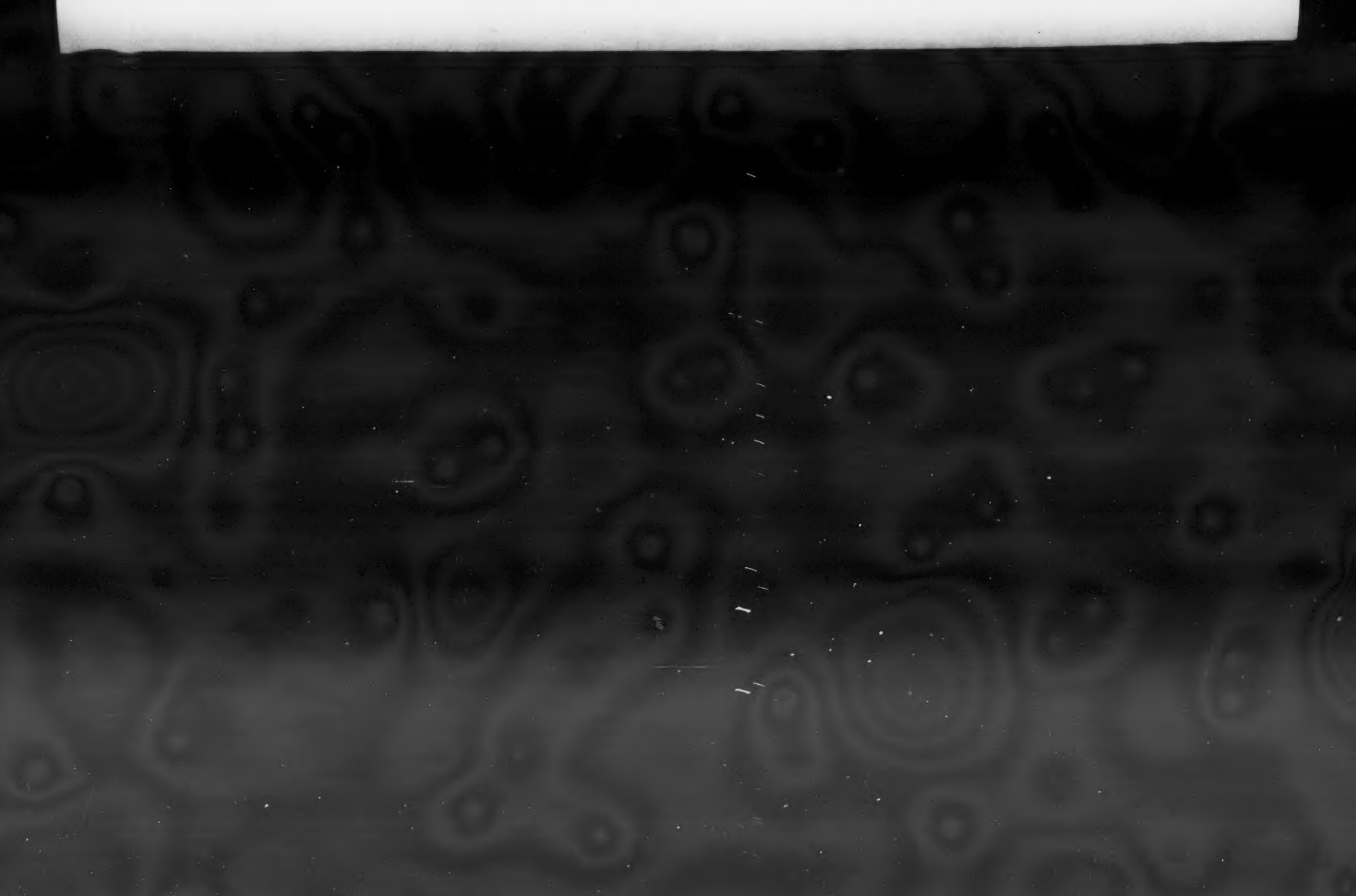

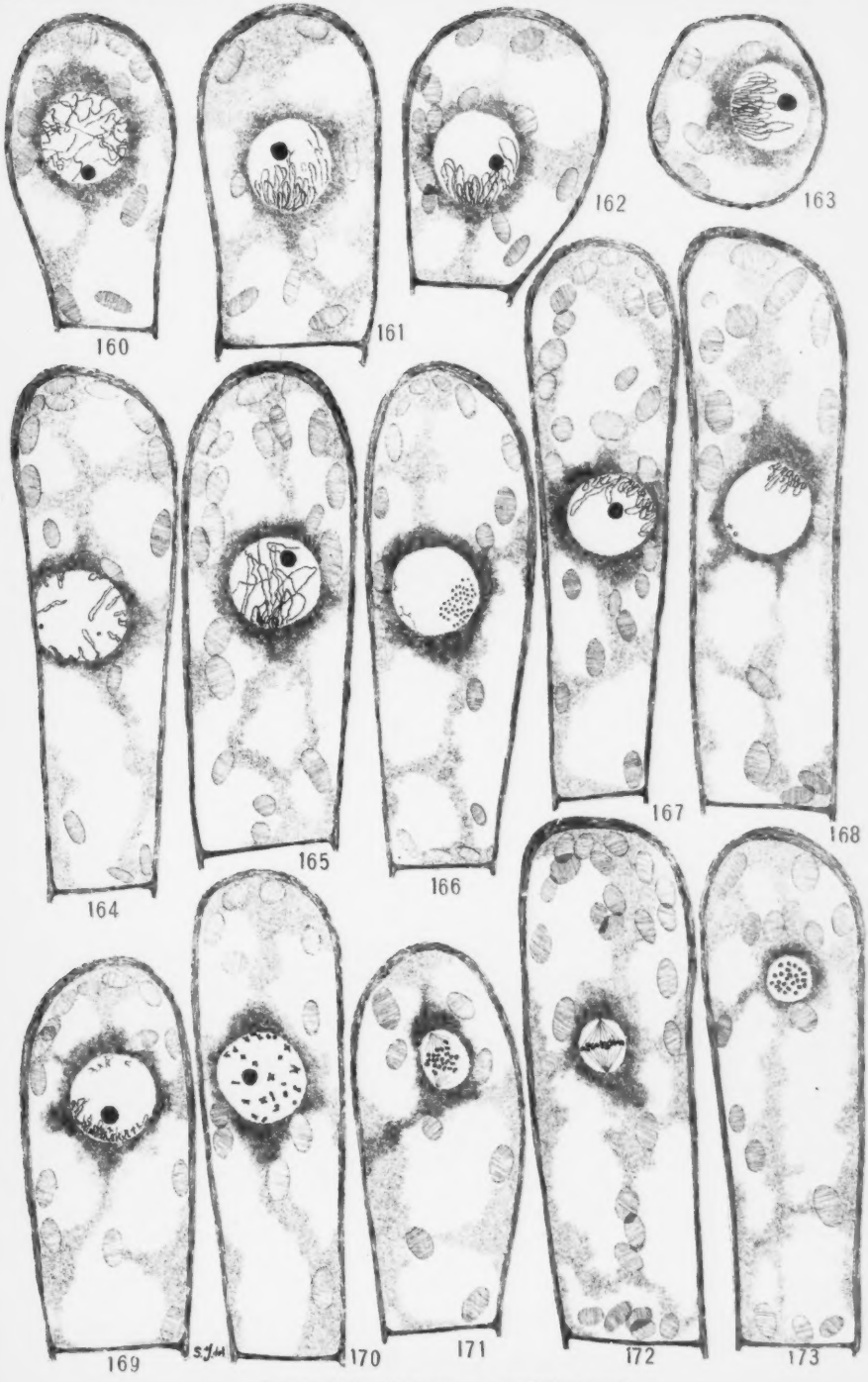

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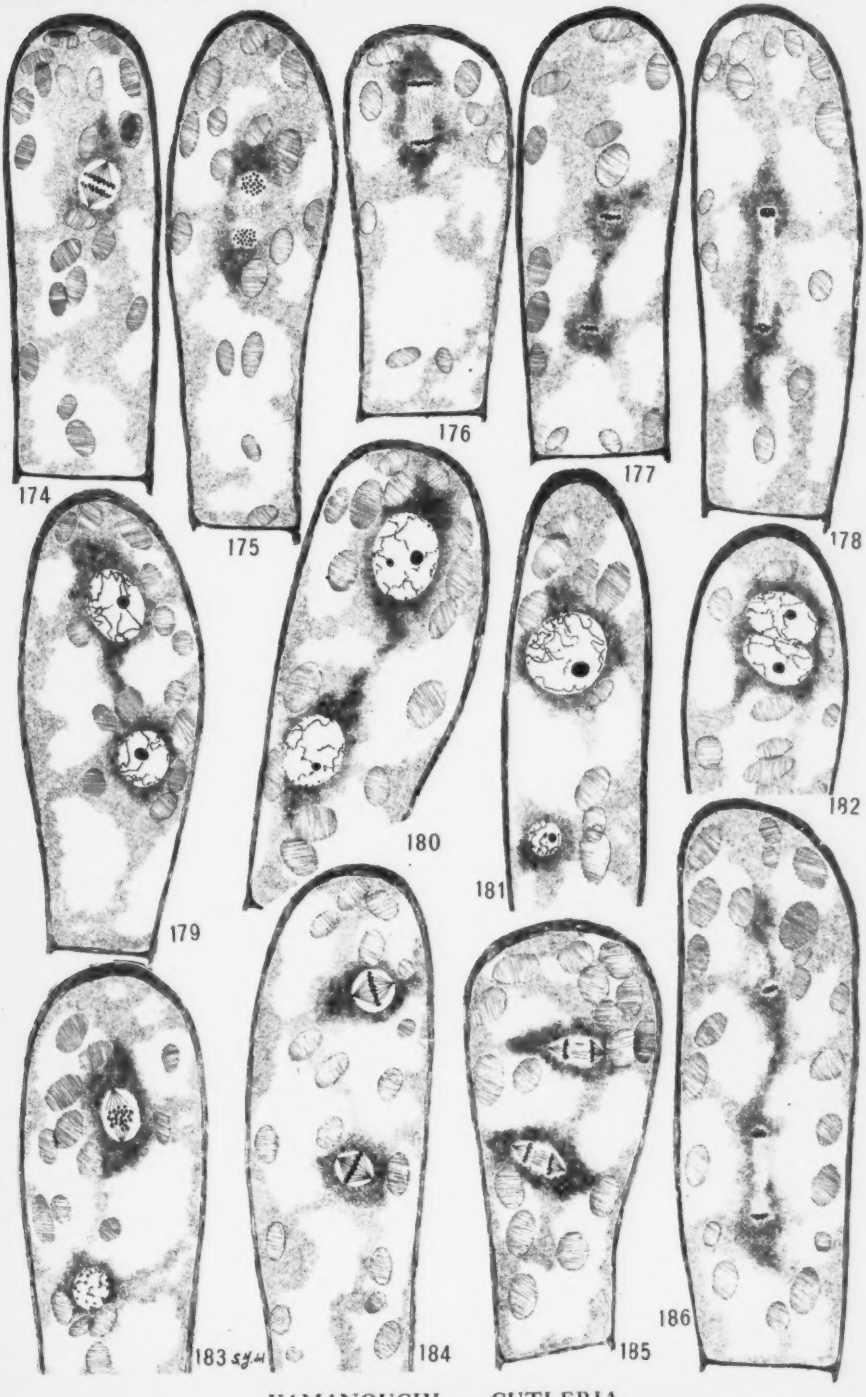

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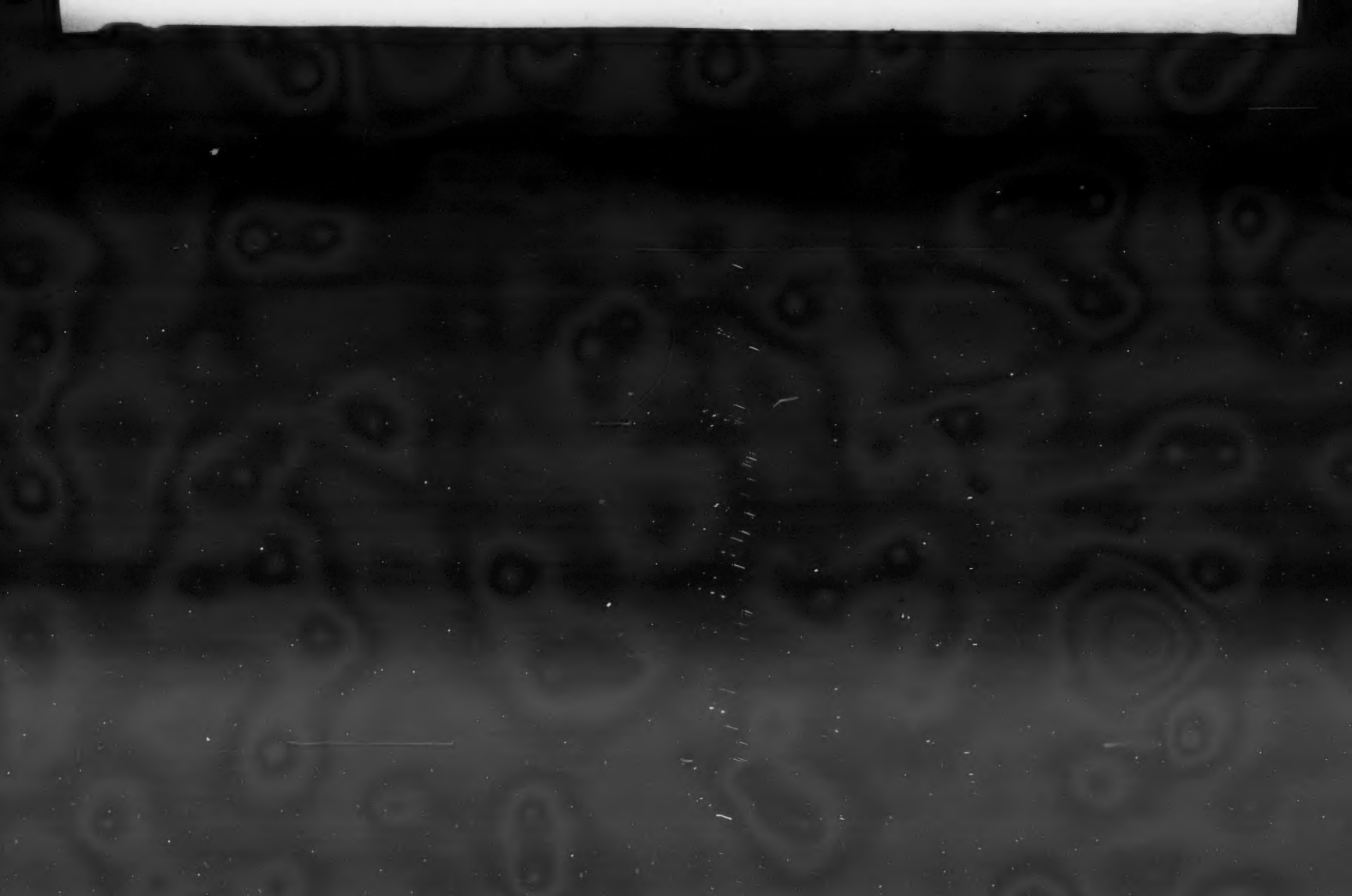

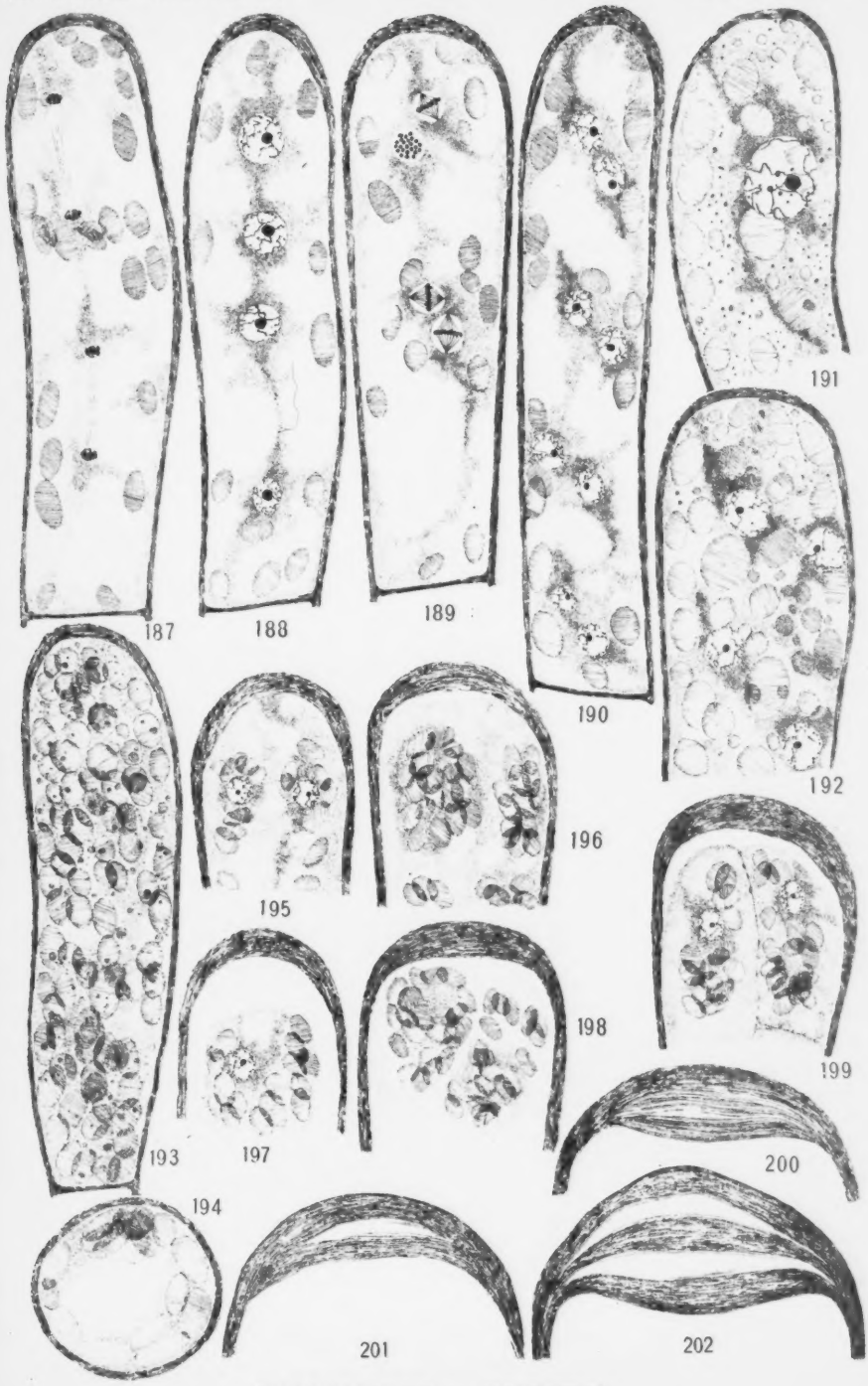

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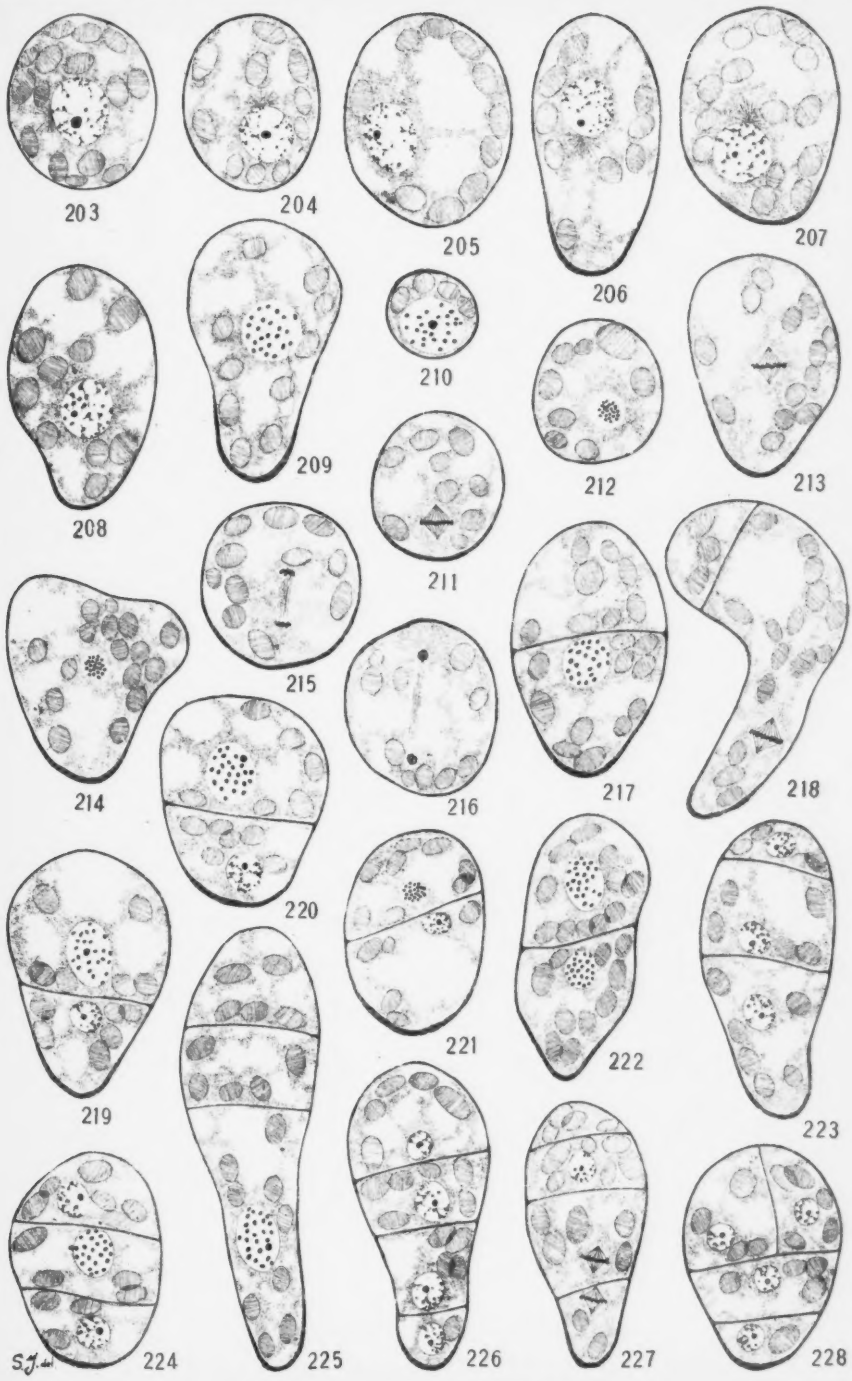

YAMANOUCHI on CUTLERIA

THE NATURE OF THE ABSORPTION AND TOLERANCE OF PLANTS IN BOGS[1]

ALFRED DACHNOWSKI

The consideration of measured physical habitat conditions,[2] which is desired as a basis for distributional relationships of plant associations, their succession and morphological distinction, and particularly for a theory of physiologically arid habitats, has not rendered clearer the nature of the absorption of plants in bogs and peat deposits. Interest in the study of the absorption and the varying degree of tolerance and resistance of plants growing in Ohio bogs has been coincident with the determination of the quantitative nature of the habitat factors, but it has been only through an appreciation of the subordinate value of the physical habitat factors that attention could be given to the special diosmotic properties of the plants and of the substances absorbed, together with the changes which the penetrating substances produce upon the plants. The changes which the substances undergo internally or externally to the absorbing cell or organ are relationships of equal importance in the problem of nutritive metabolism, but a discussion of them cannot be attempted as yet.

The evidence as to the rôle of physical and biotic habitat factors, derived from study of bog vegetation in its relations to the substratum, temperature, and evaporation, from consideration of the relation of bog vegetation to the chemical nature of peat soils,[3] need not be reviewed here in detail. It pointed to something else than merely the atmospheric influences as ecological conditions for the development of bogs and for the selection and growth of plants tenanting such areas.

[1] Contribution from the Botanical Laboratory, Ohio State University. No. 71. Read before the Botanical Society of America at the Washington meeting, 1911.

[2] DACHNOWSKI, A., The vegetation of Cranberry Island (Ohio) and its relations to substratum, temperature, and evaporation. BOT. GAZ. **52**:1–33, 126–150. 1911.

[3] ———, The relation of Ohio bog vegetation to the chemical nature of peat soils. Bull. Torr. Bot. Club **39**:53–62. 1912.

The evaporation in a bog forest averages 8.1 cc. daily and shows a close correspondence to the record obtained by others for a beech-maple forest.[4] In a bog meadow the rate (10.9 cc. daily) is less than that for the open campus of the State University (15.8 cc. daily). As far as local atmospheric conditions are concerned, the rate of evaporation is not a sufficient cause to determine succession of vegetation, nor are the differences in the rates efficient limiting factors.

The rôle of substratum temperature is obviously not the most direct factor in southern localities contributing to the causal relation between water requirements of bog plants and available supply. Neither has the coefficient of the differences between soil and air temperatures a greater value in the selection of plants for bog areas, or in their root functions.

The concentration of mineral salts in bog water from various plant associations ranges between 40 and 160 parts per million; the acidity of the solutions varies from less than 0.00075 to 0.004 normal acid, when titrated with NaOH. There seem to be no free "humus" acids. The acid reaction noted can be attributed to adsorption phenomena,[5] especially to the selective absorbent power of the cell colloids of disintegrating plant tissue which retain, as BAUMANN and GULLY[6] have shown, chiefly the basic ions of dissolved salts. The osmotic pressure of the solutions in the various associations is very nearly alike in the several plant zones and about the same as that of lake and river water. The differences cannot be associated with factors limiting the distributional relationships and the activity of plants in bogs.

Variations in the position of the water table do not influence the character of the vegetation, nor do they offer an explanation of the xerophytic structure of the plants, for the peat mat upon which the more typical bog xerophytes and heath associations succeed one another is more often a floating mat and moves with any change

[4] TRANSEAU, E. N., The relation of plant societies to evaporation. BOT. GAZ. 45:217–231. 1908.

FULLER, G. S., Evaporation and plant succession. BOT. GAZ. 52:193–208. 1911.

[5] CAMERON, F. K., The soil solution. 1911. p. 55.

[6] BAUMANN, A., und GULLY, E., Über die freien Humussäuren des Hochmoores. Mitt. K. Bayr. Moorkulturanst. 1910. pp. 31–56.

in the water table of the lake. In such a mat differences in the rate of the movement of water through peat soil do not exist, and hence are out of the question in the problem of the supply and the rate of removal of water by plants.

The chemical analyses of Ohio peat soils, the data of which appear elsewhere,[7] show wide variations, but there is a certain uniformity in the range. When a correlation between the chemical character of peat and the respective bog vegetation unit is attempted the well defined relations are these:

In poorly decomposed bog meadow peat the percentage of volatile matter is high, the percentage of fixed carbon, nitrogen, and ash is low; the reverse is true for the well decayed peat supporting a bog forest and deciduous trees.

Peat soils from various plant associations in bogs contain the essential mineral salts such as potash, phosphoric acid, and others, in inconsiderable quantities—only a fraction of 1 per cent. The salts, it seems, play only a minor rôle for protoplasmic activities, and in the growth and ripening of bog plants. Tolerance and resistance of plants to bog habitat is not an osmotic relation; it cannot be related to a greater resistance to water absorption produced by high external osmotic pressure, nor, it seems, to the lack of some one salt in the mineral content of the soil or in the plants. The ash content of the wood of bog trees is less than 0.5 per cent, with an occasional maximum of about 1.5 per cent.

The solubility of the coarsely fibrous peat from bog meadows is less than that of peat in more advanced stages of decomposition supporting genetically higher associations of plants. The quantity of nitrites, nitrates, and ammonia is very small and yet amply sufficient to support luxuriant growth. Practically all the substances in solution are transition products of proteins and carbohydrates arising through the action of obligate microorganisms. Bacteriological investigations have shown clearly the importance of biological processes. As a source of food to the microorganisms and in the nature of the organic compounds produced during the partial digestion of the upper layer of the vegetable débris, the substratum constitutes an efficient limiting and selective factor.

[7] DACHNOWSKI, A., The peat deposits of Ohio. Geol. Surv. Ohio, Bull. 16, 1912 (in press).

Now that it has been possible to show the inadequacy of various of the physical environmental relations of plants in bogs to account for the failure of some of the agricultural plants to thrive and for the survival of others; and since differences in light-intensity, in special absorptive powers of roots for peaty substrata, in fungal mycorhiza, and in morphological limitations in the absorption and in the conduction of water do not enter into the problem with the agricultural plants used for the test experiments, it seems timely to consider in more detail the specific rôle of the organic decomposition products in the relation between the required quantity of available water and the quantity absorbed by the plants.

That some sort of regulatory, reciprocal mechanism, acting within certain limits, is of the utmost importance in these species seems evident from the fact that while the presence of structural modifications is generally regarded as reaction in favor of a bog vegetation, the most noteworthy characteristic which enables invading plants to resist the unfavorable conditions is a greater elasticity of functions and perhaps some specific place function. What is the mechanism connected with the failure of many agricultural plants to thrive in peat soils and in solutions of bog water? What critical features, either as products of habitat or congenital variation, do the surviving plants possess to regulate or control the absorption of injurious organic bodies, and what are the pathological aspects which involve dwarfing, leaf-fall, and general senescence in most invading species alien to the habitat?

A knowledge of the limits of functional variation within a known species and its several varieties should prove very essential as to the rôle and the range of the individual and genetic differences in the plants themselves, and the ability of the plants to inhibit the absorption of deleterious bodies, or to neutralize the injurious action of the substratum.

In the present preliminary paper data are submitted which were obtained from experiments in the laboratory with several standard varieties of grain sorghums, alfalfa, and bean. The seeds were obtained from the United States Department of Agriculture through the office of seed distribution. The seeds were germinated in sterilized quartz sand and employed in a manner

described in earlier papers. The physiological tests were made in bog water from the central (cranberry-sphagnum) station on Cranberry Island at Buckeye Lake, Ohio. All experiments were made in duplicate series. Paper-covered "Mason" jars were used containing 500 cc. of untreated bog water. The following selected series in tables I to III is especially suggestive and typical.

The tables show at a glance which of the varieties is the more efficient in counteracting the effects of injurious organic compounds. Not only the relative transpiration quantities but also the morphological effects as shown by the general appearance of roots and leaves bear out the observation that the rate of entrance of water is as high and higher than the transpiration rate. The evaporating power of the air during several of the experiments was relatively high.

Especially in bog water of greater toxicity than that of the date in the above series, the plants were in strong contrast to each other. The rate of growth varied considerably according to the amount of transpiration and to the supply of available water. The decreased permeability of the plasmatic membrane of the root-hair cells favored their efficiency in selective absorption and in growth. When the rate of transpiration decreased, the root tips and the tops made but slight growth. The roots were discolored for some distance from the tip, appeared gelatinous, and not only their surface but the meristematic tissue seemed injured, inhibiting the formation of new laterals. The leaves were short and unfolded imperfectly. At the beginning of the experiment the roots of the stronger plants were able to counterbalance the injurious action to a slight extent; light brown insoluble bodies appeared deposited upon the surface of the roots. In dilute solutions of bog water the roots remained white. Invariably, however, the toxicity was lessened most in plants whose ability to counteract the harmful effects was most pronounced. The plants functioned less readily, and their rate of reaction diminished as the active mass of bacterial products increased.

A characteristic behavior became evident in the increase of green weight of the plants in the dilute solutions, and in the observation that this effect was far from being uniform in all the cultures. The

deleterious action of bog water was, on the whole, less marked upon the tops than upon the roots. Nevertheless the green weight of some of the plants with a lower transpiration value was greater than that of the plants transpiring more strongly. Examples are numbers 3, 5, and 7 in table I; 2 and 5 in table II; 4 and 6 in table III; 7 and 10 in table IV.

TABLE I

TRANSPIRATION DATA OF VARIETIES OF GRAIN SORGHUMS[8] IN BOG WATER
MARCH 6–24, 1910

Variety of sorghum	Transpiration in grams	Green weight produced	Water required for 1 gram of green matter
1. Milo	106.15	2.59	40.95
2. White Durra	91.05	2.18	42.98
3. Dwarf Milo	86.70	2.87	30.17
4. Dagdi Durra	78.95	1.89	41.70
5. White Kowliang	78.32	2.92	26.08
6. Blackhull Kaffir	69.95	1.40	49.85
7. Brown Kowliang	55.65	1.46	37.98
8. Red Kaffir	52.90	1.28	41.34

Atmometer: 25 cc. daily average

TABLE II

TRANSPIRATION DATA OF VARIETIES OF ALFALFA IN BOG WATER
MAY 6–26, 1910

Variety of alfalfa	Transpiration in grams	Green weight produced	Water required for 1 gram of green matter
1. Medicago falcata	11.50	1.48	7.77
2. Var. 16399 (Washington)	11.86	2.28	5.20
3. Var. 23625	8.72	0.99	8.80
4. Var. 9359 (Turkestan)	7.32	0.59	12.40
5. Sand Lucerne 20457	11.93	2.21	5.40

Atmometer: 18.9 cc. daily average

It is quite generally known that rapid growth is usually accompanied by active respiration, and hence slowly developing plants are able to increase in dry weight upon a smaller quantity of water absorbed and transpired. It seems clear from the normal appearance of the roots of these plants, that the injurious substances have an entirely different effect upon some varieties of the plants with

[8] BALL, C. R., The history and distribution of sorghum. U.S. Dept. of Agriculture, Bur. Plant Industry, Bull. 175, 1910.

the smaller transpiration value from that observed in others. The marked difference is undoubtedly due to the nutritive value of the assimilable organic compounds. This particular feature of variability in nutritive metabolism is so characteristic and strik-

TABLE III

TRANSPIRATION DATA OF SPECIES AND VARIETIES OF BEANS IN BOG WATER
FEBRUARY 24–MARCH 11, 1910

Species and varieties	Transpiration in grams	Green weight produced	Water required for 1 gram of green matter
1. Dolichos 22025	150.68	3.75	40.18
2. Dolichos 8542	99.54	1.52	65.61
3. Phaseolus mungo var. 18310	66.46	1.34	49.59
4. Var. 17096	69.98	2.32	30.16
5. Phaseolus mungo	56.35	1.24	45.32
6. Guar	36.57	1.21	32.23

Atmometer: 7.3 cc. daily average

TABLE IV

TRANSPIRATION DATA OF WHEAT PLANTS IN SOLUTIONS OF STERILIZED BOG WATER AND PEAT, INOCULATED WITH BOG BACTERIA
MARCH 31–APRIL 15, 1910

Culture	Transpiration in grams	Green weight produced	Water required for 1 gram of green matter
1. C. 19 b.+f	12	1.16	10.37
2. C. 15	8.90	0.80	11.12
3. D. 20	14.90	1.14	13.07
4. C. 13	13.08	0.94	13.91
5. C. 7	15.65	0.98	15.96
6. C. 16	15.25	0.93	16.39
7. C. 19 (fungus)	17.93	1.60	11.20
8. C. 17 (fungus)	17.40	1.01	17.22
9. C. 9	18.07	1.06	17.04
10. C. 21 (fungus)	27.33	2.36	11.58
11. Alder tubercles	50.31	2.20	22.86
12. Mixed culture of above	67.48	1.92	35.14

Atmometer: 11.7 cc. daily average

ing in agreement with the several experiments which were conducted, that analyses with reference especially to the ratio between the carbon and nitrogen content of the plants are much to be desired. Experiments on the availability of nitrogen in peat have been made by a number of workers, but mostly upon sun-dry or

kiln-dry peat, the solubility of which in water is very low. The results confirm, however, both an increase in the production of dry matter in plants, and of dry matter relatively richer in the amount of nitrogen, as compared with the percentage in plants from soils lacking peat.[9]

Additional evidence of a similar nature is derived from experiments of more recent date with pure cultures of isolated bog organisms growing in sterilized solutions of bog water and peat (table IV, nos. 7 and 10), and from the preliminary work upon peat composted with the bacterial life from stable manure. They confirm the earlier experiments and also demonstrate the ability of some mycelial bog fungi and the organisms in alder tubercles[10] to increase transpiration and green weight of wheat plants about 200 per cent above that in untreated bog water. Normal appearance is here associated with a uniformly higher absorption of the solution, amount of transpiration, and green weight produced, and with the healthy condition of roots and leaves. The wheat plants in the cultures have the usual osmotic pressure isotonic with about a 0.2 to 0.3 normal potassium nitrate solution. Difficulty in absorption and tolerance or the xerophytism in bog plants do not seem to be correlated with high osmotic pressure.[11]

The point of most importance which should be noted in this connection is the obvious difference in the water requirements of the plants. Water and its solutes, whether organic compounds or inorganic salts, are as a general rule taken up in a different ratio from that existing in the substratum. The existing differences in the various colloids of cells would naturally tend toward inequalities in the amount of water or solutes absorbed and held by the tissues of the different varieties of species; the diosmotic properties of the protoplasmic membrane, differing according to the species

[9] HASKINS, H. D., The utilization of peat in agriculture. Massachusetts Sta. Rept., pt. 2:39–45. 1909.

LIPMAN, J. G., Report of the soil chemist and bacteriologist of the New Jersey Agricultural Experiment Station. 1910. pp. 188–195.

[10] SPRATT, E. R., The morphology of the root tubercles of *Alnus* and *Elaeagnus* and the polymorphism of the organism causing their formation. Ann. Botany **26**: 119–128. 1912.

[11] FITTING, H., Die Wasserversorgung und die osmotischen Drukverhältnisse der Wüstenpflanzen. Zeitschr. f. Bot. **3**:209–275. 1911.

used as an indicator, would further determine the difference and variability in absorption, resistance, or tolerance. Inasmuch as the amount of mineral salts in bog soils and the amount used in the growth of bog plants is very small, and since the lack of larger quantities is not a factor in the succession of bog associations, the most fundamental distinction is that which controls the supply of available water. A method of determining the ratio between ash and the yield in organic compounds on the basis of the water requirement of plants for the period of their growth would have the merit of convenience, and, it must be admitted, the accuracy which is often questionable in the unit employed and as preferably expressed in agricultural literature. The unit of water requirement now used in agricultural texts for ten different economic species is 450 pounds of water for one pound of dry matter produced. Data of that character do not place the classification and comparison of soils, correlations with fertility or with age of plant, maximum growing period, and seasons on a measurable basis. The unit is numerically inaccurate and does not express the fundamental and causal relations.

Experiments upon the transpiration value of bog plants in relation to structure and habitat, to be published later, have shown that the data cannot always be expressed satisfactorily in the gm^2h system. Transpiration is a reciprocal relation. It is affected by the conditions which react upon the absorbing roots, and it is associated with chlorophyll activity and the absorption of carbon dioxide in the vertical gradient. Transpiration in the lower, more humid stratum of a bog meadow is often slight for days at a time. The luxuriousness of the vegetation and the amount of dry matter produced do not vary in this case with the transpiration quantity, but with protoplasmic permeability and the specific metabolism, permitting of exchanges by solubility, and with the active enzymic agents within the cells which effect the assimilation or the destruction of the substances in the external medium. Whatever the cause of the differential permeability,[12] solubility

[12] CZAPEK, F., Über eine Methode zur direkten Bestimmung der Oberflächenspannung der Plasmahaut von Pflanzenzellen. Jena. 1911.

LEPESCHKIN, W. W., Zur Kenntnis der chemischen Zusammensetzung der Plasmamembran. Ber. Deutsch. Bot. Gesells. **29**: 247–260. 1911.

of the substances in the medium and in the plasmatic membrane is prerequisite to penetration (osmosis) into the living cells.

In previous publications on the factors by which the present bog vegetation is determined the writer pointed out that different species of cultivated plants show marked differences in the degree of sensitiveness to the toxic conditions of a bog habitat. That the stunted plants in these experiments have not lost their capacity for absorption and growth can be readily demonstrated. The plants resume their natural functions as soon as they are placed in dilutions less fatal in its effects. In contrasting the differences in physiological activity it was further shown that various phases of absorption and transpiration resulted from the progressive addition to the medium of chemically inert filtering materials. Types of soil were used ranging from the weathering products of soil-forming rocks to the completely oxidized products characteristic as the final residue. Incidentally it was shown that the normal growth of the plants in the uncontaminated soils was replaced by an abnormal retardation. In the main the study indicated that upon extraction of the injurious substances by means of insoluble adsorbing bodies, not only the differences between different species as to their tolerance and resistance were less pronounced, but also the differences in toxicity existing between the several zones within the same habitat. The selective action of the habitat was shown to be greatly diminished upon the removal of the injurious organic substances accumulating in the peat substratum. The conclusion was drawn that the relative power in bog plants for absorbing or rejecting the injurious constituents of bog soils and bog water was therefore the limiting factor, controlling the survival value of invading species and of plants native to the habitat. The roots of bog xerophytes are not much shorter than those of other plants; the lateral roots develop extensively, and the prevalent direction of root growth is horizontal rather than downward. This reaction cannot be regarded as one due to low soil temperature or to a slight oxygen content. The inhibitory factor for root growth which increases with depth is the reducing action of the substratum and the incomplete disintegration of organic compounds. It is now well known that certain root enzymes are oxidizing agents

which assist in the destruction of deleterious compounds in soils of an organic nature, and that the oxidizing action becomes lessened when the injurious organic substances are in excess. The wide variations in this functional reaction are probably of greater importance than external factors. It seems a tenable hypothesis, therefore, that the survival or the extinction of invaders may depend more upon the degree of functional plasticity than is generally admitted.

The experiments here cited furnish nothing more than an indication of the relative importance of some of the factors involved. The weight of evidence is obviously incomplete, for numerous important considerations have received no attention whatever in the present paper. The problem of absorption is not one of simple solution, but an intricate and coordinated process, and much needs to be known of the energy relations between plants and habitat and the organization of the protoplasmic membrane of absorbing organs. From the present study the following relations may be summarized:

1. Physiological investigations of peat soils have brought out clearly the fact that the character of the obligate bacterial flora and the nature of the organic compounds produced form a very important factor in the relative fertility of peat soils, in the causes of vegetation succession, in the distributional and genetic relationships of associations, and in the characteristic xeromorphy of both ancient and modern bog vegetation.

2. In view of the widely differing behavior of agricultural varieties in a bog water solution, and the interesting observation that the plants respond differently to the same solution, the conclusion is inevitable that here the source of the difference must logically be looked for not in the solution alone, but in the condition of the plants as well.

3. Since certain of the organic compounds eventually penetrate the protoplasmic membrane of absorbing organs and inhibit growth, it is evident that much importance must be ascribed to the influence exerted upon the plasmatic membrane, to the consequent differences in its diosmotic properties, and to the pathological changes induced which accompany the absorption of the injurious substances.

4. Some plants in contact with peat soil solutions may cause the organic constituents to be precipitated in an insoluble form.

5. In other plants the different organic carbon and nitrogen compounds arising in peat through the activity of microorganisms may be absorbed and assimilated. The chemical formula and transpiration data alone afford no indication of the physiological importance of the substances, hence the nutritive value of these compounds should be estimated on the basis of the total water requirement of a plant during its period of growth and the ratio between carbon, nitrogen, and ash in the plant.

6. The phenomena of absorption and tolerance of plants in bogs deal plainly not with osmotic pressure relations so much as with considerations of the permeability of the absorbing protoplasmic membrane, its power of endurance, and its ability by enzymic action either to absorb and assimilate or to transform injurious bodies into insoluble, impermeable compounds.

7. The organic disintegration substances in peat soils, while inhibitory to agricultural plants, have little or no effect upon certain xerophytic plants. It is concluded, therefore, that they may be positive forces not only in producing the natural succession of vegetation in bogs, but also in determinating xeromorphy and the associated relation of the members, within each group, which best succeed upon peat deposits. These organic substances play the differentiating rôle and are a cause of the infertility of peat deposits even when the amount of air and water in the soil is abundant and the temperature and humidity conditions are favorable to growth.

It is needless to point out that these facts have an important bearing on the agricultural exploitation of peat deposits and on the subject of the proper value of peat land to agriculture.

It is a pleasant duty to record my thanks to Mr. M. G. DICKEY and Mr. M. COROTIS for their assistance in obtaining the transpiration data in tables I to III.

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INGROWING SPROUTS OF SOLANUM TUBEROSUM[1]

C. STUART GAGER

(WITH PLATE XXXVI AND SIX FIGURES)

Description

As is well known, it is not at all uncommon to find tuberization of the sprouts on potatoes kept over winter in a cellar. The fact is commonly attributed to the absence of light and the dampness of the cellar. In the late fall of 1907, a large basket of potatoes, of the "Green Mountain" variety, was placed, for want of a cellar, in an unheated chamber. There was one east window in the room,

1 2 3

FIGS. 1–3.—Fig. 1, Various stages of tuberization of the sprouts of a potato under conditions of diffuse illumination; fig. 2, Young tubers emerging from within an old seed tuber of *Solanum tuberosum* (cf. figs. 1, 4, and 5); fig. 3, Cross-section of a tuber of *Solanum tuberosum* with ingrown sprouts.

and the curtain was ordinarily up, so that the room was neither dark nor damp. On the contrary, the atmosphere of the room was comparatively dry. Under these conditions, a number of the potatoes were found with sprouts in various stages of tuberization, varying from a slight enlargement back of the tip to well formed "potatoes" (fig. 1), but in the case of two or three of them, the

[1] Brooklyn Botanic Garden Contributions. No. 5. The substance of this paper was given before the Botanical Society of America on December 29, 1911.

sprout-tubers appeared to be emerging through the skin from within the potato (fig. 2). Closer observation and dissection disclosed the interesting fact that at least a quarter or a third of the potatoes, of which there was about a bushel in all, had ingrowing sprouts. The condition is well illustrated in fig. 3, which is a typical cross-section.

On careful dissection of many of the tubers, the ingrowing sprouts were found to ramify in every direction throughout the

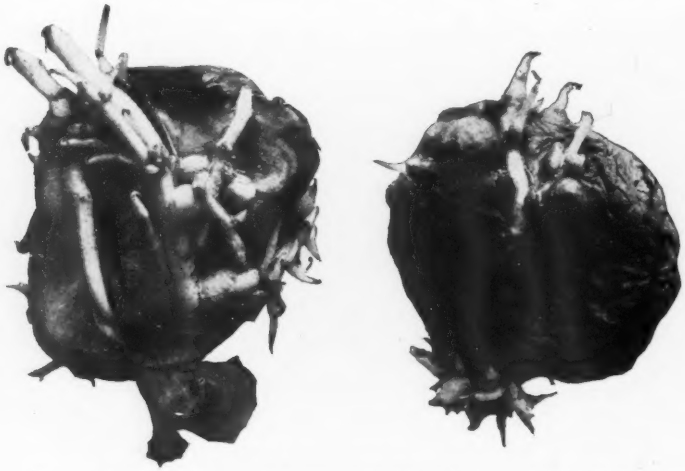

FIG. 4.—Tubers of *Solanum tuberosum* with ingrowing sprouts: the figure at the right shows the ingrown sprouts emerging through the skin; the figure at the left is of a dissection, showing rootlets, the marked development of lenticels, and the tuberization of some of the branches of the ingrown sprouts within the old tuber (cf. figs. 2 and 5).

tissue of the potato. The atrophied and etiolated bud end retained the characteristic nutation curvature, but the sprout was frequently more or less enlarged just back of the tip (figs. 4 and 5). Lenticel-like openings were well developed in the epidermis of the sprouts, often giving them the appearance of a cylindrical file.

Numerous fibrous roots grew out from the branches, and they seemed, for the most part, to be confined in their growth to the channels made by the stem. As is clearly shown in the right hand

potato of fig. 4, the internal sprouts would often grow through the skin and emerge at various points.

The branches tuberized freely, and it was not uncommon to find five or six, or even more, well formed, but pure white, tubers of various sizes entirely within the old tuber. In some cases, as in the right hand specimen of fig. 5, the branches were only imperfectly tuberized, and the tip retained its nutation curvature. Often, as noted above, the young tubers, like the unswollen branches, had pushed through the skin of the potato and, where exposed to the air, had developed a characteristic brown epidermis (fig. 4).

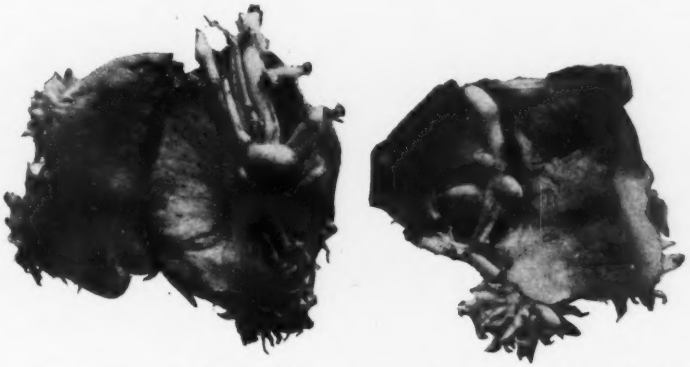

FIG. 5.—Dissected tubers of *Solanum tuberosum*, showing various stages of tuberization of branches of ingrown sprouts, both within and without the seed tuber (cf. figs. 2 and 4).

In many instances there was every *appearance* of a reversal of polarity of the sprout. This is clearly shown in fig. 6, which illustrates two "eyes," the one at the left of a normal potato, the one at the right of one of the abnormal ones. What has occurred in the latter *appears* to be just the reverse of what took place in the former: roots occur at the distal end of the sprout, where we would ordinarily expect the terminal bud, and the numerous branches appear to have developed from the proximal end of the sprout. Whether this is actually the case or not one hesitates to say. It is possible that the entire shoot system, shown at the right in fig. 6, may have developed from a sprout whose tip turned through 180°

toward the surface of the potato and penetrated the parent tuber from without. But it is only the a-priori improbability of a reversal of polarity that makes the writer hesitate to declare it. The evidence clearly indicates it, but the evidence is not all in.

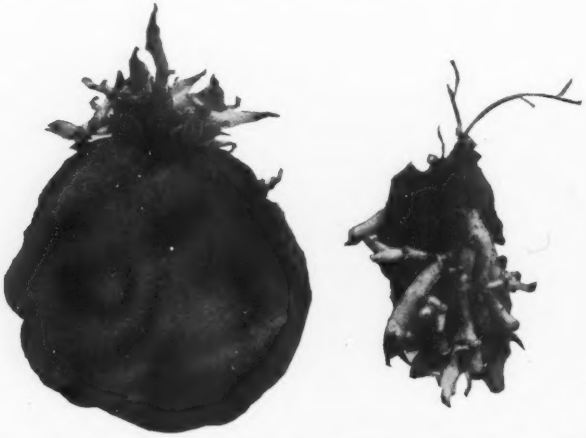

FIG. 6.—Sections through sprouting tubers of *Solanum tuberosum:* at the left, a normal "eye"; at the right, an "eye" with sprouts ingrown and indicating a reversal of polarity of the branch.

Discussion

What caused the ingrowing of these sprouts it is difficult to say. The fact that the potatoes were stored in a room where the air was much drier than that of cellars, where potatoes are usually kept, suggests that the low humidity was at least a contributory cause. But equally interesting is the question of how the sprouts made their way through the tuber. Were the channels through which they grew formed by the digestion of the potato tissue by an enzyme secreted by the tip of the sprout; or did the channels result merely from the mechanical pressure of the sprout as it elongated?

It will be recalled that a similar problem arose in connection with the endogenous emergence of lateral roots. Considerable difference of opinion has existed on this question. The first physiological study of the emergence of lateral roots appears to have been made in 1871, by REINKE (9), who stated that the channel

through the cortex was digested by a substance secreted by the emerging root. The same conclusion was reached later by VON HÖNE (**12**) and by VAN TIEGHEM (**11**). Neither REINKE's nor VAN TIEGHEM's figures, however, show evidence of enzymatic action. In 1896 CZAPEK (**1**) reported that he found in the excretions of the roots of higher plants no evidence of any enzymes. If they are present, the amounts are too small to be detected. PFEFFER has declared for a mechanical *modus operandi*, aided by some activity on the part of the cortical tissue.

In 1894 PEIRCE (**6**) found that the roots of *Vicia* and *Pisum* penetrated living tissue by mechanical pressure, unaided by enzymes. He also states that the radicle of *Pisum* could enter through the uninjured periderm of a potato from the outside. In 1903 OLUFSEN (**5**) reported a confirmation of PEIRCE's results, but POND (**8**) was unable to confirm them, and reported negative results also for *Vicia Faba* and *Lupinus albus*. When the periderm was wounded, the radicles of these seedlings entered easily and penetrated the parenchymatous tissue. When the periderm was unwounded, the radicles deeply indented the surface, but never pierced through. Microscopic examination showed that the periderm cells, and, to a less degree, the hypodermal cells also, were compressed, but there was no evidence of corrosion. "The advancing root formed callus, but when the periderm is wounded the callus does not form. . . . . "

In one of POND's experiments a potato tuber was cut in two and the outer surfaces placed together and held firmly in this position by string. Then a channel was made in one half to within a few millimeters of the skin, and the radicles of seedlings inserted. The whole was then incased in gypsum. The radicles perforated the periderm of the first half from the inside, and were thus brought into contact with the outside of the periderm of the other half, but this they failed to penetrate. From these observations POND concludes that the mechanical push is too weak to accomplish penetration from without. "Microscopical examination of the flesh of a potato showed no evidence of any digestive action."

In a similar manner POND found that an elongating radicle of *Lupinus albus* was unable to penetrate through the uninjured

epidermis of another *Lupinus* radicle. The second radicle was always deeply indented, but no signs appeared of corrosion of the surface. If the surface was even very slightly wounded, as for example by pricking it with a fine glass point, then the other radicle easily entered and passed entirely through without callus formation. The penetrating root, however, was never found to pass through the central cylinder, but always around it, thus indicating more resistance than that offered by the cortex. The cylinder was indented, but there was no evidence of corrosion of its cells. Starch grains did not appear digested either by autolysis or by the entered root. The results of mechanically forcing a glass rod into the tissue could not be distinguished from those produced by an entering radicle. The conclusion drawn was that the mechanical push was not sufficient to pierce the cuticle from the outside, and that "if the radicle or the lateral root secretes an enzyme, such enzyme has no digestive action upon the cuticle."

As in the case of the roots, so with the potato, the course of procedure for a solution of the problem is clearly indicated. If the channels were the result of enzymatic action we would expect to find, first, in the tips of the sprouts an enzyme able to digest the potato tissue; second, evidence of enzymatic action in the tissue itself; third, absence of any evidence of mechanical pressure; and finally, we might expect to find the epidermis of the ingrowing sprout modified in the direction of glandular epithelium. If the sprout merely pushed its way through the tissue of the tuber, we would find no signs of enzymes or of enzymatic action, but rather positive indication of mechanical pressure.

Physiological and anatomical study

A considerable quantity of tips of the ingrowing sprouts was given to Professor WILLIAM J. GIES, of Columbia University, who kindly offered to have them tested for enzymes. While waiting for a report on this test, microscopic sections of the sprouts were examined, to see if there was any modification of the epidermis in the direction of a glandular epithelium, such for example as that on the scutellum of the embryo of *Zea Mays*. As is clearly shown in *A* and *B* of plate fig. 1, a well developed columnar epithelium was

found, and since the epidermal cells are more nearly isodiametric in normal sprouts, it was expected that the chemical examination would disclose the presence of enzymes. Such however was not the case. No enzymes were detected, and this experience emphasizes the truth that any inference as to the function of an organ or tissue, based upon structure alone, cannot always be relied upon, unless substantiated by positive evidence.

Further confirmation of the absence of enzymatic action was obtained by examining microscopic sections of the walls of the channels made by the sprouts in the tissue of the tuber. There were no signs of corrosion of the cell walls nor of the starch grains within the cells (plate fig. 2).

Only one alternative remained: the sprouts made their way through the tissue of the tuber by mechanical pressure alone. This conclusion found abundant confirmation. The wall cells of the channels made by the sprouts were greatly compressed by the advancing tip (plate figs. 2 and 4). In light of the studies made on the mode of emergence of lateral roots, it is instructive to compare plate figs. 3 and 4. This latter figure is a detail of the tissues at the point marked *C* in plate fig. 1. Fortunately, at this point a lateral root had begun to develop, and it is clearly seen (fig. 3), not only that the walls of the cortical cells show no signs of enzymatic action, but that they are evidently compressed by the advance of the developing root tip. The paths of the ingrowing sprouts and of emerging lateral roots are evidently made in the same manner, namely by mechanical pressure alone, unaided by enzymatic action.

Experimental production of ingrowing sprouts

But how did the ingrowing sprouts start? Do they, as suggested above, represent normal sprouts that for some unexplained reason turned their tips toward the tuber and penetrated through the skin? There is no evidence for this view. In numerous cases where the "eyes" were deeply indented, small sprouts grew out laterally until their tips came into contact with the skin of the potato. But, as in the case of POND'S attempt to cause one root of *Lupinus* to penetrate another held firmly at right angles to it, so here the surface of the potato was indented by the tip

of the sprout, but no case of penetration was observed. At the writer's suggestion, Miss LUCILE KEENE,[2] then a senior in the University of Missouri, endeavored to secure the penetration of one potato by the sprouts of another. The two tubers were bound tightly together with stout cord, and buried in moist sphagnum. In no case were the sprouts successful in penetrating through the uninjured skin of the adjacent tuber, though the latter was indented. However, if the sprouts were placed against the cut surface of another potato, they entered easily, made their way through the parenchymatous tissue to and *through* the skin at the farther surface. That the sprouts can easily penetrate the cortex from within, though not from without, was shown by the abnormal cases where such penetration was general (fig. 4). Had enzymolysis been a factor, the sprouts might as easily have penetrated from without. The experiments with roots, as noted above, gave analogous results.

The observed facts will not admit of a definite denial of reversal of polarity. Many of my dissections cannot reasonably be interpreted in any other way, but it still seems possible, though not always probable, that the ingrown sprout arose as a lateral branch starting at the very base of the main sprout and *below the skin of the tuber*. This hypothesis at least does not make as large a draught on pure faith as one involving the conception of a reversal of polarity in the shoot. DETMER (**2**) long since called attention to the fact that while the intensity of polarity varied greatly with different species, it was especially well marked in the case of *Solanum tuberosum*.

The cause of tuber-formation

What caused some of the ingrown sprouts to form tubers? The answer to this question is of course bound up with the larger question as to why potato branches ever tuberize. The literature bearing on this problem was discussed by the writer (**3, 4**) in 1906, and need not be reviewed here. Reference may again be made, however, to the suggestion of BERNARD that the formation of tubers is due to a species of *Fusarium*, endotropic with *Solanum tuberosum*.

[2] Miss KEENE also found a similar case of ingrowing sprouts in Montana, but the sprouts were only slightly branched, and formed no tubers within the old potato.

This suggestion was tested experimentally by JUMELLE, but with negative results. Quite evidently this factor does not enter in the tuberization of branches of the ingrown sprouts. GOEBEL cites tuber-formation as an illustration of "qualitative correlation," stating that it is a function of the relation of the branch to the whole shoot system, its underground position, and the material supplied to it.

It seems to the writer that an attempt to explain such a deep-seated character as the formation of tubers by potato plants is like trying to explain the cornness of corn. We may ascertain experimentally what external conditions or combination of circumstances must be realized in order that tubers may result, but that they form at all is because the plant is *Solanum tuberosum*, rather than *Pisum sativum* or *Solanum Dulcamara*. To use a recent and very valuable terminology, the formation of tubers by *Solanum tuberosum*, or by any other tuber-forming species, under suitable environmental conditions, *is an expression of the genotypical constitution of the plant*. Further explanation than this lies far in the future.

Conclusion

1. Ingrowing sprouts of *Solanum tuberosum* make their way through the tissue of the tuber not by enzymatic digestion of a channel in the tissue, but by the mechanical pressure which accompanies growth in length.

2. Potato sprouts do not elongate with force sufficient to penetrate through the uninjured "skin" of the potato tubers from the outside, but they easily penetrate the skin from the inside.

3. A reversal of polarity in ingrowing potato sprouts is not definitely demonstrated, but there is evidence pointing to this conclusion.

4. Tuberization of branches takes place freely on ingrown sprouts of *Solanum tuberosum*.

5. The formation of tubers on *Solanum tuberosum* is a function of external conditions plus the genotypical constitution of the species.

THE BROOKLYN INSTITUTE OF ARTS AND SCIENCES
BROOKLYN BOTANIC GARDEN

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EXPLANATION OF PLATE XXXVI

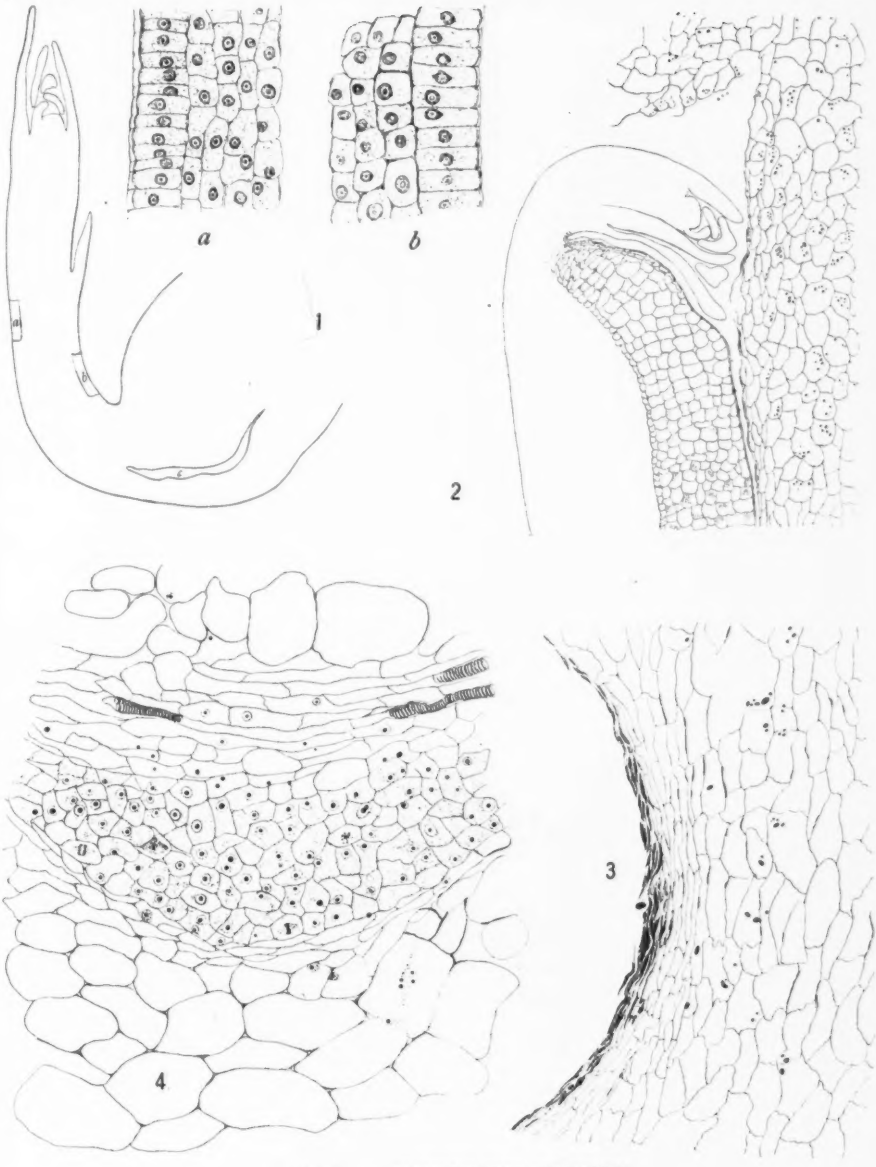
Solanum tuberosum

FIG. 1.—Outline of a longitudinal section of an ingrown sprout: *A* and *B*, cellular structure at the regions marked *A* and *B* in the outline, showing well developed columnar epithelium.—Zeiss oc. 4; obj. D.

FIG. 2.—Longitudinal section through the tip of an ingrown sprout, with adjacent tissue of the seed tuber, showing mechanical compression of the cells of the tuber by the growing sprout and absence of any evidence of corrosion of either cell walls or starch grains; the breaks in the cell walls are artifacts; many of the starch grains have fallen out of the section.—Cf. figs. 3 and 4.—Zeiss oc. 4; obj. AA., lower lens only.

FIG. 3.—Early stage in the development of a root within an ingrown sprout; this section was taken at the area marked *C* in fig. 1; note the compression of the cortical cells by the advancing root.—Cf. figs. 2 and 4.—Zeiss oc. 4; obj. AA.

FIG. 4.—Cross-section through a seed tuber, showing compression of the wall cells of a channel made by an ingrown sprout.—Cf. figs. 2 and 3.—Zeiss oc. 4; obj. AA.



GAGER on INGROWING SPROUTS

THE ABORTIVE SPIKE OF BOTRYCHIUM

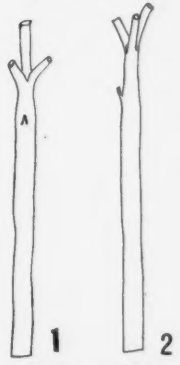
CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 164

O. O. STOLAND

(WITH TWENTY-ONE FIGURES)

Interest in the study of the vascular anatomy of the Ophioglossaceae has increased since CHRYSLER'S work[1] on the nature of the fertile spike appeared in 1910. He made the vascular supply of the leaf the basis for concluding that the fertile spike represents two fused basal pinnae. The nature of the vascular supply of the abortive spike has so far received no special attention.

This investigation was undertaken to determine the origin and nature of the vascular supply of the abortive spike, and to compare it with that of the sterile pinnae and the fertile spike. CHRYSLER found that the series of changes undergone in the origin of the strands to the sterile pinnae were precisely the same as those for the fertile spike.

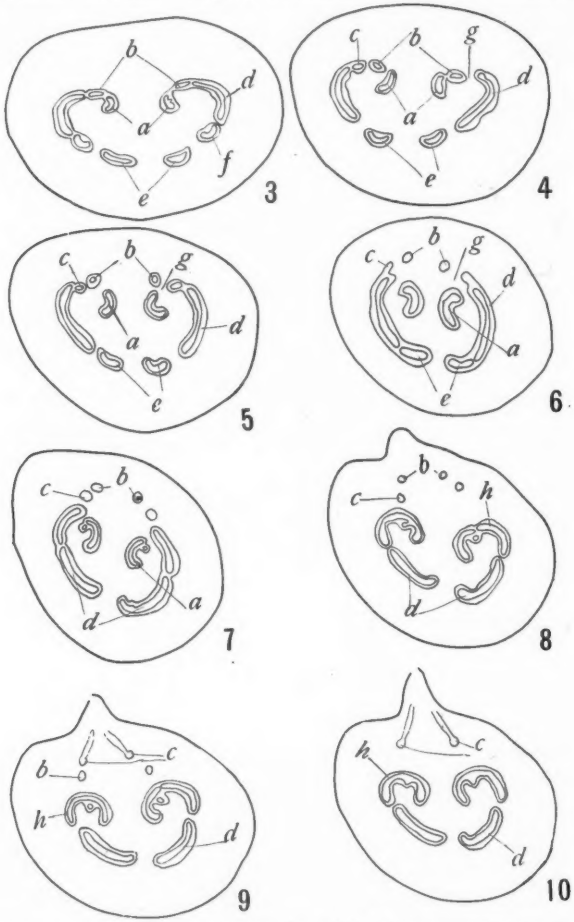


FIGS. 1, 2.—Fig. 1, adaxial view of the petiole, with the abortive spike and first pair of pinnae cut off; one-half natural size; fig. 2, lateral view of same.

The material studied was *Botrychium virginianum*, the species from which CHRYSLER made his figures illustrating the origin of the strands to the fertile spike and sterile pinnae. The abortive spike is of very common occurrence in this species. It appears on the adaxial side of the petiole as a minute structure about 2 cm. below the first pair of sterile pinnae (figs. 1, 2). The fertile spike, however, always comes off from the main axis slightly below the first pair of pinnae. The elongation of the petiole after the abortive spike separates from the axis leaves it some distance below the first pair of pinnae.

[1] CHRYSLER, M. A., The nature of the fertile spike in Ophioglossaceae. Ann. Botany 24:1–18. *figs. 1–16. pls. 1, 2.* 1910.

Serial sections were made throughout the petiole from about 8 cm. below the abortive spike to the place where the first pair of sterile pinnae appear. Figs. 3–10 show the changes undergone in

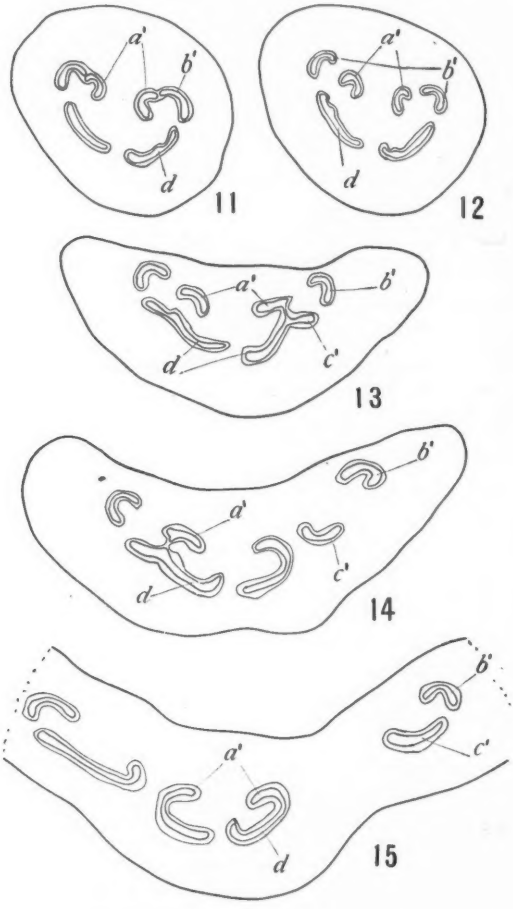


FIGS. 3–10.—Diagrams illustrating the origin of the vascular strands to the abortive spike, made with the aid of an Abbé camera lucida and reduced one-half in reproduction: distances below abortive spike as follows: fig. 3, 7.6 cm.; fig. 4, 5.3 cm.; fig. 5, 2.1 cm.; fig. 6, 4 mm.; figs. 7 and 8, about 1 mm.; figs. 9 and 10, opposite the abortive spike; adaxial side of petiole placed upward; ×15.

the vascular strands relative to the supply of the abortive spike. The vascular strands are all of the concentric type throughout the aerial part. About 8 cm. below the abortive spike the leaf trace consists of three pairs of strands (fig. 3, *d*, *e*, *f*), one large lateral pair (fig. 3, *d*), and two pairs on the abaxial side (fig. 3, *e*, *f*). One of the pairs (fig. 3, *f*) soon unites with the abaxial margin of the lateral strands (fig. 4). The second pair (fig. 3, *e*) remains free to within 1 cm. of the abortive spike, where it also unites with the abaxial margins of the lateral strands (fig. 6). The vascular strands of the abortive spike originate about 8 cm. below the point where the spike leaves the petiole. The adaxial arms of the lateral strands become hooked (fig. 3) and soon a curved strand (figs. 3–7, *a*) is cut off so that a gap is left in the sides of the leaf traces (figs. 4–6, *g*). From each side of these gaps a small strand breaks off to supply the abortive spike (figs. 4–8, *b*, *c*). The outline of these strands appears below the gap, so that they really originate from its base (fig. 3, *b*).

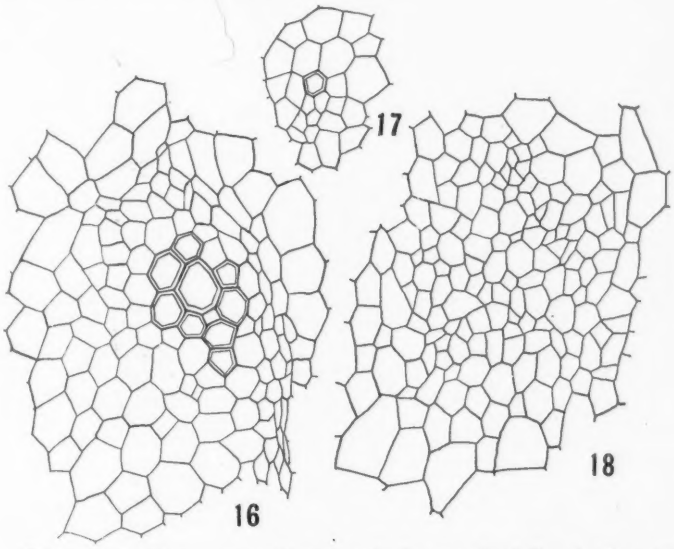
There are then four strands, that is two on each side, that supply the abortive spike. They adhere to the sides of the gap for some distance, but finally break off, one 5 cm. (figs. 4, 5, *b*), the other about 2 cm. (fig. 7, *c*) below the abortive spike. From this point they remain as separate strands running along the gap and finally enter the abortive spike (figs. 9, 10, *b*, *c*). The gaps in the lateral leaf traces close about 4 mm. below the abortive spike (fig. 8). At about this point the two lateral traces (fig. 8, *d*) each divide into two equal strands. The adaxial strands thus formed are hooked (figs. 8–10, *h*). These adaxial hooked strands each divide into two equal parts (fig. 12, *A'*, *b'*) of which the outer pair (*b'*) diverge to pass out to the pinnae (figs. 11–15, *b'*). Another pair of strands (figs. 13, 14, *c'*) arise from the adaxial margin of the lateral strand (figs. 13, 14, *d*), so that each pinna has two strands. Where these strands (*c'*) leave the leaf trace the gap becomes closed, strand *a'* uniting with strand *d*. The leaf trace above the origin of the first pair of pinnae consists of two lateral strands (fig. 15, *d*). By a study of figs. 3–15 it will be seen that the same series of changes occurs in the origin of the vascular supply of the sterile pinnae as for the abortive spike.

In some of the leaves examined the vascular supply of the abortive spike consisted of a single pair of strands, that is, one from each side, but in such cases there were two pairs of strands for



FIGS. 11–15.—Diagrams following the series shown in figs. 3–10, illustrating the origin of strands which supply the first pair of sterile pinnae; fig. 11, 5 mm. above abortive spike; fig. 12, 1 cm. above it; figs. 13–15, opposite the point where the pinnae diverge.

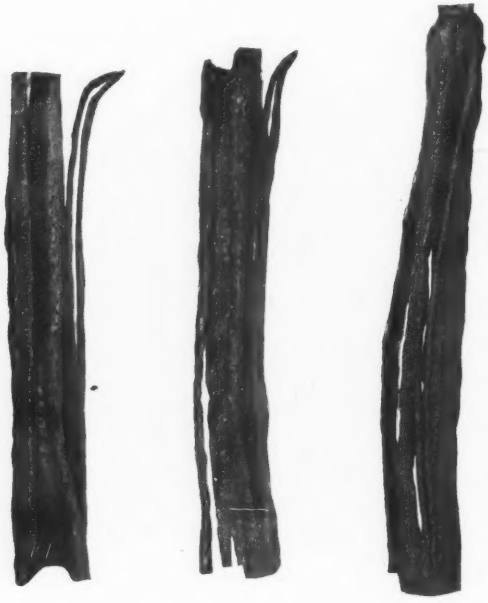
each pair of sterile pinnae. As shown in figs. 16–18, the strands of the abortive spike may have well developed primary xylem in the lower stretches (fig. 16), but farther up the xylem gradually fails to appear (fig. 17), and before they turn outward no xylem is formed. Here the strands are distinguished by their narrow elongated cells. In other cases no traces of xylem could be found throughout strands of the abortive spike.



FIGS. 16–18.—Transverse sections through the strands of the abortive spike, showing development of xylem; fig. 16, 12 mm. below abortive spike; fig. 17, 4 mm.; fig. 18, 3 mm.; ×210.

If figs. 3–15 are compared with CHRYSLER's figures showing the origin of the strands to the fertile spike, it becomes evident that the changes are essentially the same. A few exceptions may be noted. The first strand (*a* and *a'*) which breaks off on the adaxial side does not unite with the inner face of the large strand as it does in the case of the fertile spike. The gaps left by the strands to the abortive spike are much more evident. These are shown in the photographs of models in figs. 19–21. These models show only one-half of the vascular supply. In fig. 19, which shows the inner

face of the lateral strand, the two strands to the abortive spike are very evident, with the long gap behind them. The gap is seen even better in fig. 20, which shows also part of the adaxial face. Fig. 21 shows the adaxial face of the model with the two narrow strands to the abortive spike obscuring the gap. Four such strands are present in the petiole, but the model shows only one-half of the



FIGS. 19–21.—Photographs of model of the leaf traces on one side of the petiole in region where strands to abortive spike originate; fig. 21, adaxial face.

vascular supply. The pinnae of the leaves bearing the fertile spike usually have only one vascular strand, while those that accompany the abortive spike have two in all cases examined.

The breaking up of the leaf traces into curved rows of bundles below the origin of the strands to the abortive spike does not occur as regularly in the petioles with the fertile spike. This condition is described by CHRYSLER for *Ophioglossum* and *Helminthostachys*,

where the vascular supply of the fertile spike is derived from curved rows of strands.

Summary and conclusions

1. The leaf trace of the petiole bearing the abortive spike consists of several bundles instead of two bundles as usually found in the petiole bearing the fertile spike.

2. The vascular supply of the abortive spike consists of two or four strands arising from the edges or the base of the gap in the leaf trace.

3. The pair of sterile pinnae following the abortive spike are supplied by two pairs of strands originating in the same way as those for the abortive spike.

4. Xylem may or may not appear in the strands to the abortive spike, but it never appears throughout the entire strand.

5. The difference between the origin of the strands to the abortive spike from those to the fertile spike is very slight.

6. The nature of the vascular supply of the abortive spike supports CHRYSLER's contention that it represents two fused basal pinnae.

This work was undertaken at the suggestion of Professor COULTER and under the direction of Dr. CHAMBERLAIN, and I wish to express my appreciation for their valuable suggestions and criticisms. I also wish to express my thanks to Dr. M. A. CHRYSLER for valuable criticism.

UVIVERSITY OF CHICAGO

PLANTS WHICH REQUIRE SODIUM

W. J. V. Osterhout

(with two figures)

It has long been customary to regard sodium as necessary for animals but not for plants. In the light of our present knowledge of the rôle of inorganic salts, it is clear that this distinction between plants and animals is of fundamental importance, if it be true in all cases; but if exceptions occur, its significance largely disappears. The experiments which are described here were undertaken in order to learn whether there are cases in which sodium is as necessary for plants as for animals.

One flowering plant was studied, and several genera of algae, among which were representatives of the green, brown, and red algae. The investigation included species from the Atlantic and the Pacific.

The method consisted in replacing the NaCl of the sea water by one of the following substances in turn: NH_4Cl, CsCl, RbCl, LiCl, KCl, $MgCl_2$, $CaCl_2$, $SrCl_2$, $BaCl_2$,[1] $MgSO_4$, and K_2SO_4. After some preliminary experiments it became evident that the best substitutes for Na are Ca, Mg, and K. An attempt was then made to get better results by using these as substitutes for NaCl in the following combinations (the figures refer to molecular proportions as shown in the table): 500 $MgCl_2$+500 $CaCl_2$, 250 $MgCl_2$+750 $CaCl_2$, 500 KCl+500 $CaCl_2$, 667 KCl+333 $CaCl_2$, 910 KCl+91 $CaCl_2$.

All the salts were carefully tested before using and were recrystallized when necessary. The water was twice distilled from glass without the use of rubber or cork stoppers; in place of these a plug of absorbent cotton was employed. The water thus produced was not toxic to such test objects as *Spirogyra* and the root-hairs of *Gypsophila*, and its quality was further shown by the fact

[1] The introduction of $BaCl_2$ and $SrCl_2$ produced precipitates of $BaSO_4$ and $SrSO_4$ which were allowed to remain at the bottom of the dish during the experiment.

that *Phyllospadix* after being transferred directly to it from the sea water lived for 47 days.

All the solutions were made neutral to phenolphthalein before being used. The material was placed in glass dishes in diffused light and kept covered to exclude dust.

The average temperature in experiments with the Pacific species was about 20° C. and was not subject to much fluctuation. In the experiments on the Atlantic coast the jars containing the plants were partly submerged in running water during the entire period of the experiment, and the temperature did not vary far from 20° C.

It is very important to avoid an excessive amount of light. The optimum must be determined in each case by experiment, but is usually less for algae than for flowering plants.

The plants lived much longer in sea water (whether natural or artificial) than in any solution in which the sodium of the sea water was replaced by some other substance. The best substitutes for Na are Ca, Mg, and K. The accompanying table shows the length of life of the plants in solutions made up with these substitutes. It is evident that we cannot say that one of these substitutes is better than another unless we also specify what plant is being experimented on. With one plant Ca fills the place of Na better than anything else, while with another K proves better; with still another Mg is better; and in still other cases combinations (for example, Mg+Ca or K+Ca) are advantageous.

Great diversity was observed among the different species in respect to their behavior toward the other substances which were employed as substitutes for NaCl. To *Phyllospadix* the substitution of Li in place of Na is much more injurious than that of Rb, but just the opposite is true of *Ulva*, while the other plants seem to be injured about as much by Li as by Rb. Similar diversities are found in the behavior of the plants toward the other salts. These facts are important in so far as they give us a clue to the specific action of salts in life processes; this subject will receive further discussion in a subsequent paper.

All the different plants agree in showing that the replacement of Na by Ca, Mg, or K, all of which are present in considerable quan-

tity in sea water, is less injurious than the introduction of such substances as NH_4, Ba, Sr, Cs, Rb, and Li.

Some attempts were made to obtain a better solution by combinations of $MgCl_2+MgSO_4+KCl+CaCl_2$ in the proportions in which they occur in sea water and also in various proportions other than those mentioned above. So far, however, no combi-

TABLE SHOWING DURATION OF LIFE IN DAYS

Culture solution	Phyllospadix Torreyi	Ulva lactuca	Porphyra perforata	Porphyra naiadum	Egregia Menziesii	Nitophyllum multilobum	Chondrus crispus
Tap water	49	23	4	..	4	..	12
Distilled water	47	27	4	..	4	..	8
Sea water	102+	134+	50+	15+	17+	18+	90+
Artificial sea water— Stock solution*							
78 cc. $MgCl_2$ .375 M, 38 cc. $MgSO_4$ .375 M, 22 cc. KCl .375 M, 10 cc. $CaCl_2$ .375 M + 1000 cc. NaCl .375 M	102+	134+	50+	15+	17+	18+	90+
Stock solution+ 1000 cc. $CaCl_2$ .375 M	56	52	16	3	5	2	12
Stock solution+ 1000 cc. $MgCl_2$ .375 M	52	52	10	2	5	2	30
Stock solution+ 1000 cc. KCl .375 M	73	21	8	1	2	1	12
Stock solution+ 1000 cc. $MgSO_4$ .375 M	47	47	8	¾	2	1	12
Stock solution+ 1000 cc. K_2SO_4 .1875 M	60	21	6	1	2	1	..
Stock solution+ 500 cc. $MgCl_2$ .375 M, 500 cc. $CaCl_2$ .375 M	52	89	10	2	6	2	12
Stock solution+ 250 cc. $MgCl_2$ .375 M, 750 cc. $CaCl_2$ .375 M	52	52	10	2	4½	2	15
Stock solution+ 500 cc. KCl .375 M, 500 cc. $CaCl_2$ .375 M	47	28	10	1	3	2	17
Stock solution+ 667 cc. KCl .375 M, 333 cc. $CaCl_2$ .375 M	73	21	10	1	3	1	12
Stock solution+ 910 cc. KCl .375 M, 91 cc. $CaCl_2$ .375 M	66	28	6	¾	2	1	8

The (+) sign denotes that the plants were alive when the experiment was discontinued.
* It should be noted that the stock solution contains no NaCl.

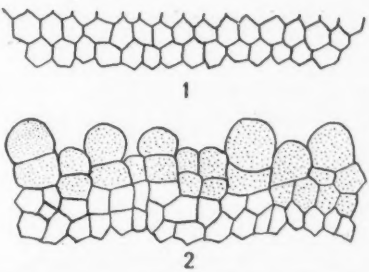
nation has been found which is decidedly better than those given in the table.

Similar results were obtained with *Gigartina*, *Ptilota*, *Iridaea*, and *Prionitis*.

Very much more striking results were obtained when experiments on regeneration were made in these solutions. Pieces of

Ulva were cut into strips and placed in the solutions. In sea water and in artificial sea water the cells along the cut edges grew and divided repeatedly, but this did not occur in any of the solutions which lacked sodium (figs. 1 and 2).

In view of these results we may conclude that for the plants studied sodium is as necessary as for animals. That its function is not merely to maintain osmotic pressure is evident from the fact that if sodium chloride be replaced by an osmotically equivalent amount of cane sugar the plants quickly die. That sodium is



FIGS. 1 and 2.—Fig. 1, portion of a frond of *Ulva* cut along one edge for experiments on regeneration; fig. 2, regeneration along the cut edge of a frond of *Ulva;* the newly formed cells are dotted; this regeneration takes place only in solutions containing sodium.

needed to antagonize the toxic action of the other salts in the solution is clear from these and previous experiments.[2] Whether sodium is needed for nutrient purposes must be decided by further experiments.

Since this investigation was begun, papers by RICHTER[3] have appeared in which he states that sodium is necessary for the nutrition of certain marine diatoms but not for that of other marine algae. Aside from diatoms his experiments seem to have been confined to a single unicellular alga. Many unicellular forms are so exceptional in their behavior that it would be unwise to draw general conclusions from experiments conducted on them alone. RICHTER states that while they grow in the absence of NaCl, they

[2] OSTERHOUT, BOT. GAZ. **42**:127. 1906.

[3] RICHTER, Sitzungsb. Kais. Akad. Wien **118**:1337. 1909.

grow much better when it is present. In his experiments only Na, K, Mg, and Ca were used, and the proportions employed were not those which exist in sea water.

Summary

Sodium is as necessary for the marine plants studied as for animals; its replacement in sea water by NH_4, Ca, Mg, K, Ba, Sr, Cs, Rb, or Li is decidedly injurious.

The best substitutes for Na are the other kations which predominate in the sea water, Mg, Ca, and K.

The behavior of various species toward certain salts indicates that each of these salts has a specific action on life processes.

LABORATORY OF PLANT PHYSIOLOGY
HARVARD UNIVERSITY

BRIEFER ARTICLES

THE PERFECT STAGE OF THE ASCOCHYTA ON THE HAIRY VETCH

It is quite well known that species of the form-genus *Ascochyta* produce a disease of the vetch, pea, and other leguminous plants. In the autumn of 1908 I collected a number of affected pods of the hairy vetch (*Vicia villosa*) which was growing on the farm of Cornell University. These were placed in a wire cage and partly covered by some leaves and grass used as a mulch for *Rhododendron maximum* in my garden. It was hoped that the perfect stage might be obtained. During early May in 1909 the cage was taken to the laboratory, and a few pods were found on which there were a number of perithecia which proved to belong to the genus *Sphaerella* (*Mycosphaerella*), although pycnidia of the *Ascochyta* were present on the same pods. They were at some distance from the perithecia, and by using care it was not a difficult matter to obtain an abundance of ascospores for making pure cultures in bean pod agar, and also for inoculation of vetch seedlings.

The germination of the ascospores was studied and the growth of the colonies was observed up to the formation of pycnidia and pycnospores identical with those formed on the vetch pods, evidence that this *Sphaerella* was the perfect stage of the *Ascochyta* of the vetch. Inoculations of vetch seedlings were made with pycnospores obtained in pure culture from sowings of ascospores. These were somewhat slow in taking, but on May 18 a few brown spots appeared on the stems, and on May 24 some of the leaves were dead and pycnidia of the *Ascochyta* were present.

On May 13 ascospores taken directly from the pods of the vetch were sown on vetch seedlings. On May 17 brownish depressed spots were present on the stems. By May 18 these spots had encircled the stem and the terminal shoot was thus killed. Again on May 15 ascospores were placed on young vetch seedlings. On May 18 a few of the leaves were dead and pycnidia were present. By May 22 the disease had spread somewhat and more pycnidia of the *Ascochyta* were formed. On May 15 pea seedlings about 10 cm. high were inoculated with asco-

spores from the vetch pods. By May 18 the edges of some of the leaves were dead and a few pycnidia of *Ascochyta* were formed. In all of these cases check host plants remained free from the disease.

The ascospores are shot out from the asci on the absorption of water. This was observed in a number of cases. While this is given as the characteristic method of escape of spores in the family Mycosphaerellaceae, the behavior of the asci and spores is not the same in all species. In this *Sphaerella* the outer, firm layer of the ascus wall is ruptured or dissolved at the apex, and the inner, thin layer then stretches out to three or four times the length of the mature ascus. When the spores are shot out through the end of this inner membrane, either successively or in a group, the inner membrane, which is very thin, collapses, while the outer layer of the wall, which does not stretch, usually remains firm.

Ascochyta occurs, usually in abundance, on the vetch, pea, and *Melilotus* in the vicinity of Ithaca. For the purpose of comparing the species on these different hosts, studying the life history and interrelationships on the different hosts, this problem was assigned in 1910 to Mr. R. E. STONE, a graduate assistant in the department of botany. This work is now completed and will shortly be published in the *Annales Mycologici*.—GEORGE F. ATKINSON, *Cornell University, Ithaca, N.Y.*

GAUTIERIA IN THE EASTERN UNITED STATES

For many years before seeing a specimen of the genus *Gautieria* I had longed to find one, since it occupies a rather unique position in the Gasteromycetes, because it is the only representative of the group in which a peridium is wanting. From the literature and illustrations I had a fairly good concept of it, and each year wished that I might have a specimen to exhibit to my classes, because it offers such an excellent demonstration of the gleba of a gasteromycete without sectioning or removing the peridium.

On October 30, 1905, Dr. A. A. ALLEN, recently an assistant in the department of zoology at Cornell University, who was then a Freshman, brought into my laboratory a small plant about the size of a marble which I at once recognized as *Gautieria*. He had collected it the previous day while on a stroll through the woods on South Hill about three miles distant from the university. Seeing an old, half-decayed specimen of *Ganoderma applanatum* lying on the ground, where it had fallen from

the trunk of a dead tree, he kicked it over and the specimen of *Gautieria* rolled out from beneath.

A few days later I organized a party of advanced students for an excursion to the locality. In the leaf mold near the dead tree we found some half-dozen other specimens. Specimens have again been found during the past summer by Mr. H. H. FITZPATRICK, one of my graduate students, who has just completed a study of its development, since he found it in all stages of growth.

Gautieria morchelliformis Vitt., of Europe, has been reported from Mexico. *G. monticola* Harkness has been described from California. The species collected in the vicinity of Ithaca I have regarded as *Gautieria graveolens* Vitt., of Europe. It has a strong, peculiar, and unpleasant odor which is characteristic of several closely related species.

The plant is attached at the base to a slender whitish rhizomorph which broadens out within the gleba in the form of anastomosing planes forming the sterile avenues which are covered with the hymenium. These make up the gleba tissue, or walls, which separate the winding chambers which open to the outside. The spores are beautifully sculptured, being longitudinally or obliquely ribbed.—GEORGE F. ATKINSON, *Cornell University, Ithaca, N.Y.*

CURRENT LITERATURE

MINOR NOTICES

Nathanson's textbook of botany.—This book[1] is written from a strictly physiological standpoint, structures receiving scant attention except as they are related to functions. The subject-matter is divided into two parts, the vegetative life and the reproduction. The first part is subdivided into (1) nutrition as a fundamental function of vegetative life, (2) the vegetative organs of the algae, (3) the structural plan of the organs of the higher plants, (4) the life history of the vegetative organs of the higher plants, (5) the orientation of the vegetative organs in space, and (6) the structure of the vegetative organs under special conditions of nutrition. The second part is subdivided into (1) reproduction in the lower plants, (2) mosses and cryptogams, (3) reproduction in flowering plants, (4) the relation between the vegetative life and reproduction, and (5) heredity. The book closes with a few remarks on the principal groups of plants.

This presentation could be read, with profit, by all classes of botanists, particularly by morphologists, who stand in greater need of such a presentation. Morphologists, however, can hardly regard the text as a "general botany," since it gives so little attention to development and phylogeny.—CHARLES J. CHAMBERLAIN.

Natal plants.[2]—The recent appearance of part 4 completes the sixth volume of this well known work. The present part contains descriptions and full-page illustrations of 25 species, most of which are of comparatively recent publication, hence little known. A brief chapter is added giving notes and corrections on plants mentioned in volumes I–VI inclusive. One species, *Brachystelma Franksiae* N. E. Brown, is new to science.—J. M. GREENMAN.

NOTES FOR STUDENTS

Physiology of lichens.—The greatest advantage to the lichen of parasitism with the alga was formerly supposed to be that the lichen received carbon which the alga obtained from the air. But now it appears reasonable to suppose that the lichen may furnish the alga a portion of the carbohydrates which it secures from the substratum. This of course cannot occur when the lichen

[1] NATHANSON, A., Allgemeine Botanik. 8vo. pp. viii+471. *figs. 394.* Leipzig: Quelle und Meyer. 1912. *M* 10.

[2] WOOD, J. MEDLEY, Natal Plants. Vol. **6,** p. 4, *pls. 576–600.* Bennett & Davis. Durban, 1912.

grows on rocks that contain no organic matter. Breathing pores have been postulated for the lichens in a general way, but we really know little about provision for exchange of gases in these plants. The student will find a general summary by FÜNFSTÜCK in ENGLER and PRANTL'S *Natürlichen Pflanzenfamilien*. In 1906 ZOFF[3] described a new *Ramalina* (*R. kullensis*) which has the so-called breathing pores well developed, and ROSENDAHL[4] in 1907 found them in *Parmelia aspidota*. Nothing more seems to have been added to FÜNFSTÜCK'S statement, and it appears probable that passages from the exterior to the interior of lichen thalli are rare instead of common.

TOBLER[5] thinks that such passages may be expected in thalli with thick cortices, but scarcely in those with thin cortices, where sufficient aeration may occur without them. He believes that the lack of sufficient air and light within the lichen thallus makes the conditions unfavorable for the alga and that this accounts for the layering of the algae near the surface of the thallus. TOBLER cultivated *Xanthoria parietina* and a number of other lichens without algae in a gelatin-beerwort medium and got a rich production of calcium oxalate. He then cultivated the thalli with the algae and was not able to find the oxalate. He supposes, therefore, that the algae used the surplus extracted from the medium by the lichen, and that the same occurs in nature, the lichen taking the oxalate from the organic substratum. We may add that according to ELENKIN'S[6] theory of endosaprophytism, the lichen may extract organic compounds from the dead algae for the living.

TREBOUX[7] is cited by TOBLER to the effect that species of *Chlorella*, *Pleurococcus*, *Cystococcus*, and some other algae investigated, are able to obtain carbon in a very different manner from that known in higher green plants. It was found that these algae are able to thrive on artificial media containing organic acids, and the conclusion was reached that they behave much like fungi with respect to carbon assimilation.

TOBLER failed to notice the excellent work of ARTARI,[8] performed on algae which grow in lichen thalli, to ascertain the physiological relationship of the

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[3] ZOFF, W., Biologische und morphologische Beobachtungen über Flechten. II. Ber. Deutsch. Bot. Gesells. **24**:574–580. *pl. 23*. 1906.

[4] ROSENDAHL, F., Vergleichende anatomische Untersuchungen über die braunen Parmelien. Nov. Act. Kais. Leop. Karol. Akad. **87**:404–459. *pls. 25–28*. 1907.

[5] TOBLER, F., Zur Ernährungsphysiologie der Flechten. Ber. Deutsch. Bot. Gesells. **29**:3–12. 1911.

[6] ELENKIN, A., Zur Frage der Theorie des Endosaprophytmus bei Flechten. Bull. Soc. Imp. Nat. Moscou II. **18**:164–186. 1904.

[7] TREBOUX, O., Organische Säuren als Kohlenstoffquelle bei Algen. Ber. Deutsch. Bot. Gesells. **23**:432. 1905.

[8] ARTARI, A., Über die Entwickelung der grünen Algen unter Ausschluss der Bedingungen der Kohlensäure Assimilation. Bull. Soc. Imp. Nat. Moscou II. **23**:39–47. *figs. 2*. 1899.

algae to the lichens. ARTARI grew *Cystococcus humicola*, obtained from the thalli of *Xanthoria parietina* and *Gasparrinia murorum*, in pure cultures on complicated media containing mineral salts or organic compounds, or in some instances both the salts and the organic matter. He found that the algae grew luxuriantly on the media containing organic matter and were dark green in color when grown in absolute darkness or in light with CO_2 excluded. On media containing mineral salts but no organic matter, the algae grew under similar conditions, but not so well. These results square beautifully with those of TOBLER, the one worker giving special attention to the lichen, and the other to the alga which lives in the thallus of the same lichen. The two researches show conclusively that the alga which lives in the thallus of *Xanthoria parietina* can obtain its organic matter as well as the mineral salts from the lichen, provided the latter grows on some other substratum than rocks that contain no organic matter.

BEYERINCK, BOUILHAC, ETARD, KLEBS, and others have obtained results with algae somewhat similar to those of TREBOUX and ARTARI, two of the authors working on a blue-green alga (*Nostoc*). *Trentepohlia umbrina* grows in the bark of trees, sometimes with lichen thalli and sometimes alone. In fact this alga bores into the bark of trees or effects an entrance through minute openings in the periderm, probably either because abundant light is not favorable to its best development, or because closer relationship with the organic matter of the periderm is more essential to its development than bright light. This alga would be an especially favorable object for such investigations as those noted above.

TOBLER also started cultures of *Xanthoria* on gelatin and transferred them to a liquid medium which contained none of the carbon compounds needed by the alga except what was in the air, and the lichen grew somewhat. The alga grew in the same liquid medium and was of normal appearance. In transferring the lichen, particles of the gelatin were unavoidably carried over. After these were probably consumed by the lichen, the alga was introduced into the culture with the lichen and grew well, but was colorless. This, he thinks, indicates that the lichen had assimilated the acid which the alga needed as a source of carbon, probably oxalic acid. He says that gelatin is not a source of carbon for the alga, so that his conclusions would not be invalidated even if the lichen had not extracted all of the gelatin from the medium before the alga was introduced.

The lichen hyphae soon entwine some of the algal cells in the culture, and thus the parasitic, or at least a symbiotic, relationship is established. TOBLER believes that the lichen obtains carbon from the alga, while the latter replaces it by extracting carbon from the oxalic acid contained in the tissues of the lichen. This means a mutual exchange of food materials between the lichen and the alga, at least as a probability. His investigation seems to indicate that the alga growing in *Xanthoria parietina* and those found in several other lichens very probably obtain their carbon from the lichen, the latter in turn

obtaining it from the organic material in the substratum. This is probably true except for lichens that grow in substrata containing no organic material and perhaps for those having thin cortices. ROSENDAHL found that thinness of cortex and presence of calcium oxalate go together in the species of *Parmelia* studied. This would indicate that the algae in lichens with thin cortices obtain their carbon from the air, and so the oxalate is stored in the lichen, while in the lichens with thick cortices the alga secures little or no carbon from the air and utilizes the oxalate obtained from the substratum by the lichen.

These investigations of TOBLER, ARTARI, and others prove that we know little regarding the nutrition of lichens and their algal hosts. The results already obtained are important and suggestive. It is to be hoped that much more work of this kind may be done.—BRUCE FINK.

Metabolism of fats.—IVANOW has published a series of papers on the metabolism of fats in higher plants. He emphasizes how little our knowledge has advanced in this field since the classical work of SACHS, and contrasts it with the advances made in our knowledge of protein metabolism in plants. IVANOW[9] believes he has established that the synthesis of fats from glycerin and fatty acids comes about through the reversible action of lipase, a view apparently well established in animal metabolism.

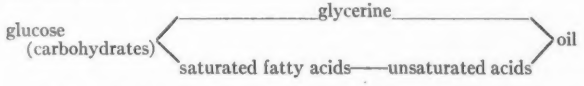
Another paper[10] deals with the transformation of fats during germination. In order to have seeds with the greatest possible variation in the nature of the fats as regards the saturation of the fatty acids involved, he used flax (very rich in fatty acids of the linoleic type: $C_nH_{2n-6}O_2$), hemp (rich in the linoleic type: $C_nH_{2n-4}O_2$), rape (rich in the oleic type: $C_nH_{2n-2}O_2$), and poppy (rich in the palmitic type: $C_nH_{2n}O_2$). In the developing seedling he finds that the intensity of consumption of the fatty acids originating from the fats is inversely proportional to the degree of saturation. The linoleic type of acid disappears first, and with it of course the hexabromide test; then follows the linoleic, oleic, and finally the palmitic types. The fall in the iodine number of the fat during germination is due to the more rapid transformation of the more unsaturated acids to carbohydrates, and not to their saturation by oxidation leading to the formation of acids with shorter chains. The acid number of the fat from each plant is a strictly determined matter, low when the fats are rich in unsaturated acids, and high when rich in saturated acids. If the constituent parts of the oil in a plant are known, one can approximate closely the acid number of that oil. The unsaturated fatty acids are largely tied up in the glyceride, while the saturated acids exist to a larger degree in the free state. The transformation of the oils during germination is by

[9] IVANOW, SERGIUS, Über Oelsynthese unter Vermittlung der pflanzlichen Lipase. Ber. Deutsch. Bot. Gesells. **29**:595–602. *fig.* 1. 1911.

[10] ———, Über die Verwandlung des Oels in der Pflanze. Jahrb. Wiss. Bot. **50**:375–386. 1912.

oxidation to carbohydrates, but the intermediate products are not known and are the next substances for investigation. Since the unsaturated fatty acids are so readily oxidized to carbohydrates (an exothermic process) during germination, the author concludes that their appearance in a plant is a special adaptation, making rapid germination possible by a great liberation of energy. As long as we know so little about the phsyiological use, if any, made of most of the energy liberated by such oxidations, this conclusion is without evidence in its favor.

A third paper[11] deals with the synthesis of fats in oily seeds. In the flax, rape, etc., the testa is formed first, followed by the development of the embryo. Pentosans accumulate early, having their only rôle in the formation of protective structures in the testa and playing no part in nutrition. The carbohydrates (glucose, cane sugar, and starch) are the main substances from which fats are synthesized; while the proteins play a minor if any part in the process. Of the carbohydrates, glucose is first used, followed by the hydrolysis and use of cane sugar, and finally starch. Intense oil formation occupies about two weeks in the middle of the seed development period. Up to the time of the beginning of oil formation, carbohydrates are stored in the stem. At this time the hydrolysis of the carbohydrates in the stem begins, and, due to their transformation to insoluble materials, oils, etc., in the seed, a falling gradient is established in that direction, causing the diffusion to the developing embryo. The first acids formed are saturated, as shown by the iodine number. The author also believes that they belong to the higher members of their respective series, for the Reichert-Meissel number is constant, and it does not vary with the acid number. It is also concluded that the volatile acids play no part in fat synthesis. The acid number varies greatly in the oil from various plants, being very low in oils from seeds rich in unsaturated acids. The author believes the following scheme shows the main features of oil synthesis in a form like the flax seed.



The variation in the iodine number with stages of development is the greater the greater the proportion of the unsaturated acids in the oil. In seeds with few fatty acid components in their oils (rape and hemp) the variation in the physical and chemical characters of the oil with stages of development is slight; while in seeds with oils of many fatty acid constituents (flax and poppy) these variations are great.

It must be remembered that such quantitative analyses cannot certainly determine the series of products and reactions involved in a synthesis, for many

[11] IVANOW, SERGIUS, Über den Stoffwechsel beim Reifen ölhaltiger Samen mit besonderer Berücksichtigung der Oelbildungsprozesse. Beih. Bot. Centralbl. **28**: 159–191. 1912.

of the intermediate products may exist in such small quantities as to escape detection.—WILLIAM CROCKER.

Endogone.—A paper by BUCHOLTZ[12] on the subterranean genus *Endogone* presents an unusually important addition to our knowledge of the group Hemiasci, established by BREFELD to include supposed transitional forms between the Phycomycetes and Ascomycetes. Further study of the forms which were originally placed in the Hemiasci has resulted in the gradual dismemberment of that group until it has lost its taxonomic status. As a result of the work of BUCHOLTZ on *Endogone*, that form also must be removed from the Hemiasci and classed with the Phycomycetes. BUCHOLTZ includes in his account 7 of the 17 species of *Endogone* (including one described as new in his paper). Two of these, *E. lactiflua* Berk. and *E. Ludwigii* Bucholtz, have a sexual process resembling that of the Phycomycetes; *E. macrocarpa* Tul. and *E. microcarpa* Tul. produce only chlamydospores; in *E. pisiformis* Link. the zygospores or chlamydospores of the other forms are represented by sporangia whose contents break up into spores as in the mucors; and in the remaining forms studied, *E. lignicola* Pat. and *E. fulva* (Berk.), the mode of reproduction is not definite. In these either sporangia or thin-walled chlamydospores are produced.

The youngest fruit bodies of *Endogone lactiflua* examined consist of a tissue of interwoven hyphae covered by an outer more firmly interwoven layer, forming a sort of peridium. Foreign hyphae occasionally penetrate the fruit body, but these are easily distinguished from hyphae of *Endogone* by their straight course and parallel walls. The hyphae of *Endogone* are sinuous in their course and have many irregular inflations. Male and female gametangia arise as saclike outgrowths of the hyphae. The nuclei in the gametangia are arranged peripherally and undergo one division. There is no differentiation of the protoplasm into periplasm and ooplasm as in the Peronosporales. A large nucleus, whose origin is not clear, appears in the center of the gametangium. The other nuclei pass toward the base of the gametangium, which is then cut off from the upper uninucleate portion by a wall. The process is the same in both gametangia. The fusion of the uninucleate gametes begins at the time of the formation of the wall. The nucleus of one gamete passes into the other gamete, but no fusion of nuclei takes place. At the apex of the fusion cell, now containing both nuclei, a portion of the wall is gelatinized, and at this point a papillate outgrowth appears, which gradually enlarges as the protoplasm and nuclei pass into it from the fusion cell. This outgrowth

[12] BUCHOLTZ, F., Beiträge zur Kenntnis der Gattung *Endogone* Link. Beih. Bot. Centralbl. **29**: 147–225. *pls. 8.* 1912. Originally published in Russian: Neue Beitr. zur Morph. und Cytologie der unterirdischen Pilze. T. I. Die Gattung *Endogone* aus d. Nat.-Hist. Museum d. Gräfin K. Scheremetjeff in Michailowskoje. Moskau **9**: 1911. See also preliminary note: Über die Befruchtung von *Endogone lactiflua* Berk. Ann. Myc. **9**: 329–330. 1911.

enlarges and forms the zygote or zygospore. The zygospore becomes surrounded by a thick wall showing differentiation into several layers. In its completed state it is inclosed in a network of hyphae whose walls fuse and become greatly thickened, forming, in cross-section, a sort of a corona around the zygospore. The nuclei were not observed to fuse in the zygospore of this species, but in *Endogone Ludwigii* a single large nucleus, supposed to be a fusion nucleus, was observed in some of the zygospores. This process of zygospore formation was observed only in the two species mentioned. In the other species the fruit body is filled with asexually formed chlamydospores or with sporangia in place of zygospores.

In his discussion the author points out the close resemblance between the sexual reproduction of *Endogone* and the mucors on the one hand, and on the other hand certain homologies between *Endogone* and the Ascomycetes. Thus in the peculiar outgrowth of the fusion cell and the paired nuclei, he sees a homologue of the ascogenous hyphae of the Ascomycetes, in some of which (as CLAUSSEN has shown for *Pyronema confluens*) the male and female nuclei do not fuse, but remain in pairs until the formation of the ascus.—H. HASSELBRING.

Position of Gnetales.—In 1911 LIGNIER and TISON published a brief statement of their view that Gnetales are apetalous angiosperms, a statement that was noted and commented upon in this journal.[13] Now they have begun the publication of an extended argument for their position, the first part dealing with *Welwitschia*.[14] A very full résumé of the literature prepares the way for a consideration of all the kinds of testimony available. The conclusions reached cannot be attacked on the basis of insufficient knowledge of the facts at hand, but of course they rest upon personal judgment as to the relative importance of the testimony, as do all conclusions in reference to phylogeny.

The general contention in reference to *Welwitschia* is that the two kinds of strobili ("inflorescences") have identical organization; that in the axil of each bract there occurs a flower of the angiosperm type, comprising five cycles of members; that the two innermost cycles form a tetracarpellary closed ovary prolonged into a long style; that the functionally monosporangiate flowers are obviously derived from more primitive bisporangiate flowers; that *Welwitschia* has retained a large number of gymnosperm characters, especially in its "anatomy and histology"; that in evolution such recondite characters change least rapidly, and therefore the phylogenetic position is to be determined by the floral characters, which are essentially angiospermous; that the great reduction of flowers and their aggregation into inflorescences do not suggest angiosperms in general, but rather a very specialized lateral phylum; that the method of specialization resembles that of the *Amentales*, and therefore *Wel-*

[13] BOT. GAZ. **51**:479. 1911.

[14] LIGNIER, O., et TISON, A., Les Gnétales, leurs fleurs et leur position systématique. Ann. Sci. Nat. Bot. IX. **16**:55–185. *figs. 40.* 1912.

witschia and *Amentales* belong to the same lateral phylum, the former at its base, the latter at its summit; that by comparing *Welwitschia* on the one hand with gymnosperms and on the other with angiosperms one may obtain a rough reconstruction of the characters of proangiosperms.

The crux of this whole argument is the interpretation given to the inner, micropyle-forming integument as of carpellary nature. If this is true, no other testimony is needed; and if it is not true, then no other testimony can show the angiosperm level. As stated in the former notice, this contention in the main brings us back to the old conflict over gymnospermy. It is clear that *Welwitschia* is a member of a reduction series, and one can imagine an open ovary derived from a closed one, for there are open ovaries among angiosperms; but it is not easy to imagine a reversion to such structures as archegonia, etc., unless proangiosperms may have retained archegonia in stages of elimination.

It will be interesting to note the disposition made of *Gnetum* and especially of *Ephedra* in the subsequent papers.—J. M. C.

Investigations on Coprinus.—WEIR[15] reports a series of miscellaneous investigations on various species of *Coprinus*. He finds that the deliquescence of these forms is brought about by the action of digestive enzymes and goes on entirely without the aid of bacteria. The digestive enzymes are most abundant when the fruit bodies approach maturity. The various parts of the fungus show considerable differences in resistance to the action of these enzymes. None of the young tissues are affected by extracts of older individuals. Parts of the gills and pileus of older plants, however, are readily dissolved, while the stems are not much affected. Other enzymes whose presence was shown by appropriate methods are tyrosinase, peroxidase, catalase, emulsin, amidase, diastase, coagulase, invertase, cytase, pectase, lipase, and rennetase.

The rest of the paper deals mostly with questions of experimental morphology, and more particularly with the relation between the capacity for regeneration of these fungi first pointed out by BREFELD, and the degree of differentiation of the regenerating tissues. It is found that in the very young fruit body the power of regeneration is not localized, but that all parts are capable of producing new plants from all cut surfaces. In the young cut stem, pilei grow out most readily from the pith, but later, when the pith has disappeared, the regenerating zone moves outward toward the periphery. In the pileus, regeneration takes place most readily at first in the region which is to become the hymenium, and later in the trama. The cuticle is not capable of regeneration. Plants whose pilei were imbedded in plaster or stems whose upper parts were thus imbedded, after removal of the pilei, produced new outgrowths along the lower part of the stems. Attempts at grafting parts of fungi on other individuals of the same species succeeded easily and gave

[15] WEIR, JAMES R., Untersuchungen über die Gattung *Coprinus*. Flora **103**: 263–320. *figs. 25.* 1911.

interesting results. All parts of *Coprinus* and other fungi exhibit distinct polarity, so that when parts of stems or pilei are grafted in their normal position on the corresponding parts of other individuals used as stocks, union readily takes place by anastamosing of the hyphae. When the part used as the scion is inserted in the reverse position, no union takes place. In partly resupinate forms, like *Polystictus*, polarity was exhibited in the same sense, but portions near the margins showed polarity to a less degree than the older parts.—H. HASSELBRING.

Lagenostoma.—This paleozoic type of seed, the first to be connected with Cycadofilicales, has been investigated further by Miss PRANKERD[16] from preparations of *L. ovoides*. The *Lagenostoma* type of seed has peculiarities that are hard to relate to the structures of the more modern gymnosperm seeds, and any additional knowledge of the facts is welcome. The structures revealed by these new preparations are described in detail, and some interesting "theoretical suggestions" are made. The seed investigated strengthens the suggestion of OLIVER and SCOTT that the outer fleshy layer of the cycadean testa represents the cupule of *Lagenostoma*, the stony layer being developed after fusion of the *Lagenostoma* integument with the cupule. The method of pollination is discussed also, and the curious supposition that extraneous water must be brought to the pollen chamber for the swimming sperms is continued. The facts in reference to the peculiar "crevice-like" pollen chamber are somewhat cleared up. It is shown that the contact of the "central cone" with the outer layer of the nucellus is quite variable, so that apparent continuity might be developed in a variety of ways. The point of this is that a preparation showing a space below and continuity aboves does not prove necessarily that the pollen chamber is being formed from below upward. In certain specimens this very appearance was observed and yet there were pollen grains in the chamber. It is not even certain that the crevice-like chamber was continuous around the central cone. The specialized apical portion of the nucellus is called the "lagenostome," and the suggestion as to its morphology is very interesting. Miss PRANKERD sees in it a modified apical annulus, which in the fossil *Seftenbergia* is a multiseriate structure, but which in living forms has become simpler. If this be true, we have a fern connection for the structure that seemed to be hopelessly advanced, namely the seed.—J. M. C.

The foliar ray of dicotyledons.—BAILEY[17] has followed up his previous work on the rays of certain groups by a more comprehensive study of the dicotyledons, resulting in some important conclusions. The primitive angio-

[16] PRANKERD, THEODORA L., On the structure of the paleozoic seed *Lagenostoma ovoides* Will. Jour. Linn. Soc. London **40**:461–490. *pls. 22–24. figs. 3.* 1912.

[17] BAILEY, IRVING W., The evolutionary history of the foliar ray in the wood of the dicotyledons, and its phylogenetic significance. Ann. Botany **26**:647–661. *pls. 62, 63.* 1912.

sperms, possessing a siphonostele with strong development of secondary wood, had uniseriate or linear rays, such as characterize the conifers. During the warmer climate of the Mesozoic, "sheets of storage tissue were built up from congeries of uniseriate rays about the persistent leaf traces of evergreen angiosperms. This primitive type of foliar ray has persisted in certain species of primitive families (Casuarinaceae, Fagales, etc.). Later changes in climate modified the storage conditions, and in the majority of living dicotyledons the aggregated units of foliar ray tissue have been diffused through the stem, and in general the evidence of their former relation to leaf traces has disappeared. In a small number of forms the primitive aggregate type has been "progressively compounded or solidified," and the result is the compound or multiseriate ray (deciduous oaks, etc.). In many families there has been a reversion to the primitive uniseriate condition. As a consequence, in the modern species the foliar ray of the primitive aggregate type has been or is being reduced, diffused, or compounded. The evidences of reduction are interesting and important in any scheme of classification. For example, *Castanea* and *Castanopsis* are reduced members of the oak family, and *Alnus mollis* and *A. acuminata* are reduced species of *Alnus*.

It is increasingly evident that the woody cylinder of angiosperms is very far from being a structure of phylogenetic simplicity.—J. M. C.

Bog vegetation.—In studying the various problems connected with the peat bogs of Ohio, DACHNOWSKI[18] has made a careful enumeration of the various plant associations involved, and traced the variously modified successions which occur. Fortunately he has not been content with observations, but has attempted various lines of quantitative study of the factors involved, such as the height and variation of the water table, the acidity of the soil, and the evaporating power of the air. He has also begun a series of chemical analyses of bog water and peat soils. The preliminary results[19] are valuable as being suggestive of lines for future investigation rather than as affording solutions for any existing problems. The chemical changes which take place in the transformation of vegetable matter into peat are only imperfectly understood, but as they are observed as exhibited in passing from the imperfectly formed fibrous material to the competely transformed structureless peat there is a relative loss of oxygen and hydrogen and an increase of carbon and nitrogen simultaneously with an increase in the reducing processes in the soils. The complexity of the problem of relating the vegetation to the chemical nature of the substratum is indicated, as well as the possible importance of the decomposition products of proteids and carbohydrates that are now beginning to be isolated and identified.—GEO. D. FULLER.

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[18] DACHNOWSKI, A., The succession of vegetation in Ohio lakes and peat deposits. Plant World **15**:25–39. 1912.

[19] ———, The relation of Ohio bog vegetation to the chemical nature of peat soils. Bull. Torr. Bot. Club **39**:53–62. 1912.

Germination of teleutospores.—In order to throw some light on the parallelism between the time period during which teleutospores are capable of germination and that during which their host plants can be infected, DIETEL[20] has, in a general way, studied some of the factors influencing the germination of teleutospores of *Melampsora*. Early in March the teleutospores of *Melampsora Larici-Caprearum* Kleb. germinate in about three days when brought into a higher temperature. The time required for germination decreases as the season progresses. Whether the shortening of the period required for germination was due to temperature changes or to a kind of after-ripening of the spores independent of the temperature was not determined. Temporary drying hastened germination. Temporary freezing did not retard the process. Strong light delayed germination. Germination takes place at temperatures as low as 6° C., and only in the neighborhood of this low point was any influence of temperature observed. Experiments with *M. Tremulae* seemed to indicate that germination in this form is less influenced by drying than in *M. Larici-Caprearum*. Germination takes place at temperatures of 6°–10° C., but proceeds more rapidly at 15°–20° C.—H. HASSELBRING.

Seedling structure in Leguminosae.—COMPTON[21] has made a notable contribution to our knowledge of seedling structure. He has examined 201 species of Leguminosae, ranging through all the regions of that vast family. The three parts of the paper present the detailed descriptions, the summarized information, and the general discussion. Under the last head the following topics are considered: the nature of the hypocotyl, hypogeal and epigeal germination, the epicotyl in the Vicieae, the level of the transition, the level of transition and the mature habit, the level of transition and phylogeny, the type of symmetry, plumular traces in hypocotyl and root, tetrarchy, reduction of the number of protoxylems, triarchy, other types of symmetry, the relationships of the types of symmetry, the size of the seedling, the primitive habit. It is obvious that in so extensive a work no outline of the results can be given, and we commend those interested to the 14 conclusions stated by the author. The closing sentence is significant: "To a limited extent, therefore, characters of seedling structure may be of diagnostic value; but it is exceedingly risky to apply them to solve the broader problems of phylogeny."—J. M. C.

Effect of tarred roads on vegetation.—With the extension of the use of gas-tar, petroleum, and bituminous substances for surfacing roads, especially in public parks, the question of injury to plants by these substances becomes one of importance. While many experiments have shown that plants are easily damaged by the fumes of tar and similar substances, such experiments

[20] DIETEL, P., Versuche über die Keimungsbedingungen der Teleutosporen einiger Uredineen. Centralbl. Bakt. II. **31**:95–106. 1911.

[21] COMPTON, R. H., An investigation of the seedling structure in the Leguminosae. Linn. Soc. Jour. Bot. **41**:1–122. *pls. 1–9*. 1912.

have as a rule been conducted from a laboratory standpoint, and have left unanswered the question of the slow action of these substances under natural conditions. From a study of the effects resulting to vegetation along the tarred roads in some of the parks of Paris, GATIN[22] finds that considerable damage is done to trees and other plants by the tar-laden dust particles; accordingly the injury is less severe along the less frequented roads. A peculiarity of the injury is that it develops very gradually, and in case of the trees did not appear until the practice of surfacing the roads with tar had been continued for two years. Dust collected from tarred roads and dusted at frequent intervals on nursery stock produced characteristic injury, consisting of spotting and browning of the leaves and retardation of growth.—H. HASSELBRING.

Cystidia as hydathodes.—As a result of a critical examination of the cystidia occurring in the hymenium and similar cystidia-like trichomes often found distributed over other surfaces of the fruit bodies of Hymenomycetes, KNOLL[23] concludes that, with the exception of certain special types like the large cystidia of some species of *Coprinus*, these two sets of trichomes belong in a physiological-anatomical sense to the same category of organs, and that they function exclusively as hydathodes. KNOLL finds that the exudation of water is restricted to a definite region, with few exceptions, situated at the apex of the trichome. The cell wall at this point is capable of swelling to such an extent that it forms a colloidal solution in the excreted water. That the drops adhering to the ends of the hydathodes consist of a colloidal solution is shown by the gelatinous residue left when the drops are allowed to evaporate on a glass slide, and also by the fact that a membrane is precipitated when the cystidium with the attached drop is immersed in alcohol. Crystals are often deposited on the ends of the hydathodes as a result of evaporation of the liquid. —H. HASSELBRING.

Plant diseases of Texas.—A survey of the plant diseases occurring within a radius of 100 miles of San Antonio, Texas, has been published by HEALD and WOLF.[24] The paper is based on collections made by the writers during a period of about two years, from 1908 to 1910. It comprises a list of fungi collected on about 200 species of hosts within the region examined, together with brief descriptions of the fungi and notes on the effects produced on the hosts. A number of well executed plates accompany the text; however, the motive that

[22] GATIN, C. L., Die gegen die Abnutzung und den Staub der Strassen angewendeten Verfahren und ihre Wirkung auf die Vegetation. Zeitschr. Pflanzenkrank. **22**:193–204. 1912.

[23] KNOLL, F., Untersuchungen über den Bau und die Funktion der Cystidien und verwandter Organe. Jahrb. Wiss. Bot. **50**:453–501. *figs. 69.* 1912.

[24] HEALD, F. D., and WOLF, F. A., A plant disease survey in the vicinity of San Antonio, Texas. Bur. Plant Ind. Bull. 226. pp. 112. *figs. 2. pls. 19.* 1912.

guided the writers in their selection of material for illustration is not clear. As a list of parasitic fungi from a region where little systematic collection has been carried on, this paper is a useful contribution. Its usefulness might have been greatly enhanced if the authors had indicated what part of their material constituted additions to the known fungus flora of Texas, and what part represented species formerly known from that region, for it can scarcely be doubted that so extensive a collection of material contains much that is new to the region.—H. HASSELBRING.

A new type of Cycadofilicales.—From a study of numerous casts, SCHUSTER[25] has described the staminate and ovulate flowers of *Schuetzia anomala* and has drawn some conclusions in regard to the position of the genus. The impressions of the staminate flowers were so numerous that it was not difficult to make reconstructions. The flower consists of 12–20 cyclic sporophylls united throughout the lower two-thirds of their length and bearing sporangia upon their inner surfaces, resembling SELLARD'S *Codonotheca* and STUR'S *Calymmatotheca*. The flowers are in a spicate inflorescence. The longitudinally striated "seeds" described by GOEPPERT are regarded as megasporophylls, and it is important to note that these megasporophylls are in undoubted connection with twigs bearing conifer-like leaves. On account of this association, SCHUSTER would make *Schuetzia* the type of a new group of Cycadofilicales, characterized by the conifer-like leaves.—CHARLES J. CHAMBERLAIN.

Root nodules of Podocarpineae.—Miss SPRATT[26] has found that root nodules are present in *Podocarpus*, *Microcachrys*, *Dacrydium*, *Saxegothaea*, and *Phyllocladus*, being modified lateral roots. A root-hair is penetrated by *Pseudomonas radicicola* (a nitrogen-fixing organism) and from thence enters the cortex. In all cases the nodules are produced by the infection of the meristematic tissue of the young lateral root before it emerges from the cortex of the parent root. Many interesting observations are made upon the stages of the bacteria and also upon the condition of the tissues of the host. The conclusion is suggested that the morphology of the nodules favors the view that *Podocarpus* and *Saxegothaea* "are the most widely divergent of the genera in the Podocarpineae, and that they are connected through *Microcachrys* and *Dacrydium*." The presence of the nodules in *Phyllocladus* is also further confirmation that the genus is related to the podocarps rather than to the taxads. —J. M. C.

[25] SCHUSTER, J., Über die Fruktification von *Schuetzia anomala*. Sitzungsb. Kaiserl. Akad. Wiss. Wien **120**:1125–1134. *pls. 1, 2*. 1911.

[26] SPRATT, ETHEL ROSE, The formation and physiological significance of root nodules in the Podocarpineae. Ann. Botany **26**:801–814. *pls. 77–80*. 1912.

Morphology of Uvularia.—Miss ALDEN[27] has investigated the life history of *Uvularia sessilifolia*, chiefly as to the sequence of events, presumably in the region of New York City. The archesporium of the microsporangium (3–6 cells) becomes differentiated the first of August, at which time also the division into parietal and sporogenous series occurs. Mature microspore mother cells were found in the middle of September, and the tetrad divisions occurred in October, so that the winter is passed with the microspores fully formed. In the latter part of the following April the division of the microspore nucleus into generative and tube nuclei occurs, and probably the former divides after the shedding of pollen. The archesporium of the megasporangium is differentiated early in March (seven months later than the microsporangiate archesporium), and consists of a single hypodermal cell which does not cut off a parietal cell. The reduction division occurs the last week of April.—J. M. C.

Spermogonium and fertilization in Collema.—Miss BACHMANN[28] has investigated *Collema pulposum* as to the nature of the spermatia and its bearing on the question of functional sexuality among the Ascomycetes. The spermatia of this species are not born in spermogonia, but few in number upon a hypha below the surface of the thallus, being completely imbedded and never set free. The carpogonia resemble those of other lichens in general structure, but the long end cell of the trichogyne does not grow toward the surface of the thallus, but more or less horizontally within the thallus toward the region of the spermatia. The attraction of the spermatia for the trichogynes is shown by the convergence of the latter about a group of spermatia. The spermatium fuses with the trichogyne to which it has become attached, and the subsequent changes are those that have been described. It seems evident that in this case the spermatia and trichogyne are functional.—J. M. C.

Seedling anatomy of Sympetalae.—LEE[29] has investigated the seedling anatomy of Convolvulaceae, Polemoniaceae, Hydrophyllaceae, Boraginaceae, Labiatae, Solanaceae, Scrophulariaceae, Bignoniaceae, and Acanthaceae. The extent of the transition region is related in a general way to the size of the seedlings, which varies greatly in different species. In the smaller seedlings the transition region is short, and the rearrangements are concluded in the upper part of the hypocotyl; while in the larger seedlings the transition region is very extended. Cotyledonary tubes occur in members of all the families,

[27] ALDEN, ISABEL, A contribution to the life history of *Uvularia sessilifolia*. Bull. Torr. Bot. Club **39**:439–446. *pls. 34, 35.* 1912.

[28] BACHMANN, FREDA M., A new type of spermogonium and fertilization in *Collema*. Ann. Botany **26**:747–760. *pl. 69.* 1912.

[29] LEE, E., Observations on the seedling anatomy of certain Sympetalae. I. Tubiflorae. Ann. Botany **26**:727–746. *pl. 68.* 1912.

but their presence seems to have nothing to do with the transition phenomena. The prevailing type of transition, present in all the smaller seedlings, is VAN TIEGHEM's type 3. Internal phloem was present in all the Solanaceae and Convolvulaceae examined, with a few possible exceptions.—J. M. C.

A disease of sugar cane.—The sugar plantations of Hawaii have suffered greater loss from an endemic disease called "iliau" than from all other fungous diseases combined. LYON, now at the Experiment Station of the Hawaiian Sugar Planters' Association, has investigated the disease[30] and finds that the causal organism is a new species of *Gnomonia* (*G. iliau*), the imperfect stage being *Melanconium*. The *Gnomonia* form is infrequent, while the *Melanconium* form is of constant occurrence. It is a leaf-sheath disease, and its attack makes it a disease of young shoots only. The entrance is effected through the leaf-bases inserted on the stem below the soil surface, and thence it extends upward and inward. The tightly packed roll of leaf-sheaths surrounding the young stem-tip is cemented into a rigid cone, so that it is impossible for the stem-tip to escape.—J. M. C.

Diaphragms in air passages.—LE BLANC[31] has reviewed the literature on the diaphragms occurring in various aquatic plants and examined other species in order to discover the origin, manner of development, and function of these organs. One of the most peculiar features of these plates is the occurrence of perforations in the form of peculiar intercellular spaces caused by the diminution of the cell contents and the consequent contraction of the cells. These perforations permit free gas exchange and yet do not greatly detract from the rigidity of the diaphragms. The diaphragms do not seem to be due to any reaction toward the aquatic medium in which the plants develop, and appear to be a portion of the mechanical tissue system occasionally containing some reserve food materials.—GEO. D. FULLER.

Algae of Colorado.—ROBBINS[32] has published a list of the algae of Colorado, which brings together all the recorded species and the additions made by the author during three years of investigation. The result is a list of 143 species, including 38 Cyanophyceae and 105 Chlorophyceae. *Spirogyra*, with 14 species, is the largest genus.

The same author[33] has investigated also the occurrence of algae in certain

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[30] LYON, H. L., Iliau, an endemic cane disease. Exper. Sta. (Hawaii) Bull. 11. pp. 32. *figs.* 10. *pl.* 1 (colored). 1912.

[31] LE BLANC, M., Sur les diaphragmes des canaux aérifères des plantes. Rev. Gén. Bot. **24**: 233–243. 1912.

[32] ROBBINS, W. W., Preliminary list of the algae of Colorado. Univ. Colorado Studies **9**: 105–118. 1912.

[33] ———, Algae in some Colorado soils. Col. Agric. Exper. Sta. Bull. 184. pp. 24–36. *pls.* 4. 1912.

soils in which *Azotobacter chroococcum* is extremely active in fixing nitrogen. By the use of cultures, which are described, 21 species of soil algae were found, all but two being Cyanophyceae, and the best represented family being Nostocaceae. It is concluded that these algae are an important source of energy for *Azotobacter*.—J. M. C.

Podozamites distans.—The fragments referred to this form, sometimes under the name of *Cycadocarpidium*, have been regarded by some as pinnate leaves, and by others as shoots with spirally arranged leaves. The megasporophylls, with two ovules at the base, bearing some resemblance to those of *Dioon*, are collected into a loose cone. Nevertheless, SCHUSTER[34] comes to the conclusion that *Podozamites distans* is a primitive conifer, coming from the same Cycadofilicales stock which gave rise to the Ginkgoales. Consequently, he would have *Podozamites* removed from the Cycadales and placed with Coniferales. SCHUSTER'S figures, as well as two of NATHORST'S which he reproduces, seem to the reviewer to favor relationship to the Cycadales.—CHARLES J. CHAMBERLAIN.

Anatomy of Equisetum.—Lady ISABEL BROWNE[35] has investigated the anatomy of the strobilus and of the fertile stem of *Equisetum*. The xylem situation in this genus is of great interest, and in the axis of the strobilus it is best developed. At the nodes, the xylem forms a ring or occurs as bands of varying width; while in the internodes the xylem breaks up into definite strands. *E. arvense*, *E. palustre*, and *E. limosum* form a series showing progressive reduction of the xylem. The study of the strobilus further confirms the view that the "sporangiophores" are not lobes of a suppressed foliar member, but are "whole appendages," which would seem to indicate that they are not sporangiophores.—J. M. C.

Stomata of Bennettites.—LIGNIER[36] has discovered the existence of stomata on the interseminal scales of *Bennettites Morieri*. The structure as figured is obvious enough, and about the guard cells there are concentric subsidiary cells. LIGNIER raises the question whether the presence of these stomata does not indicate freedom for the movement of air among scales and ovules, and therefore less compactness of structure than develops later, when the seeds mature and the tips of the interseminal scales hypertrophy. Since stomata occur within the ovaries of angiosperms, as *Lilium* for example, their presence does not prove the free circulation of air.—J. M. C.

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[34] SCHUSTER, JULIUS, Bermerkungen über *Podozamites*. Ber. Deutsch. Bot. Gesells. **29**:450–456. *pl. 17*. 1911.

[35] BROWNE, ISABEL M. P., Contributions to our knowledge of the anatomy of the cone and fertile stem of *Equisetum*. Ann. Botany **26**:663–703. *pls. 64, 65. figs. 10*. 1912.

[36] LIGNIER, O., Stomates des écailles interséminales chez le *Bennettites Morieri* (Sap. et. Mar.). Bull. Soc. Bot. France **59**:425–428. *figs. 2*. 1912.

Classification of plants.—A third edition of Professor BESSEY's *Outlines of plant phyla* has appeared. The previous editions were noted in this journal (**51**:317. 1911; **53**:275. 1912) and the general features of the classification given. In the new edition the 14 phyla remain the same, but the families have increased from 648 to 652. The relation of the conventional four great groups to this scheme may be indicated by the statement that the thallophytes are broken up into 7 phyla, the bryophytes remain as a single phylum, the pteridophytes become 3 phyla, and the spermatophytes 3.—J. M. C.

Perithecium of Polystigma.—BLACKMAN and WELSFORD[37] have investigated the development of the perithecium of *Polystigma*, and have discovered that while well marked ascogonia occur, they disorganize without producing ascogenous hyphae, and that the spermatia are also functionless. It differs from most of the Ascomycetes in which the normal sexual process is absent by the fact that both sex organs are distinctly produced, but that both are abortive.—J. M. C.

Wound reactions in fern petioles.—HOLDEN[38] induced wound reactions in the petioles of 37 species of ferns, the wounds being thin superficial shavings made with a scalpel in three regions: the curled apical portion, the region of pinna insertion, and the region below pinna insertion. Various reactions were obtained, which differ too much in details to be summarized in a review, but all of which are interesting contributions to the subject of wound reactions.—J. M. C.

Mycorhiza of Asarum.—SCHWARTZ[39] has studied the mycorhiza of *Asarum europaeum*, finding it limited to the cortical region abutting on the steles of young roots. Thick-walled swellings were found on some of the hyphae, representing a resting stage.—J. M. C.

Lateral archegonia in Pinus.—SAXTON[40] has made the very interesting discovery of a female gametophyte of *Pinus maritima* which bears two lateral groups of two archegonia each, and no terminal (micropylar) archegonia at all.—J. M. C.

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[37] BLACKMAN, V. H., and WELSFORD, E. J., The development of the perithecium of *Polystigma rubrum* D.C. Ann. Botany **26**:761–767. *pls. 70, 71.* 1912.

[38] HOLDEN, H. S., Some wound reactions in filicinean petioles. Ann. Botany **26**:777–793. *pls. 73, 74. fig. 1.* 1912.

[39] SCHWARTZ, E. J., Observations on *Asarum europaeum* and its mycorhiza. Ann. Botany **26**:769–776. *pl. 72.* 1912.

[40] SAXTON, W. T., Note on an abnormal prothallus of *Pinus maritima* L. Ann. Botany **26**:943–945. *fig. 1.* 1912.

GENERAL INDEX

Classified entries will be found under Contributors and Reviews. New names and names of new genera, species, and varieties are printed in **bold face** type; synonyms in *italic*.

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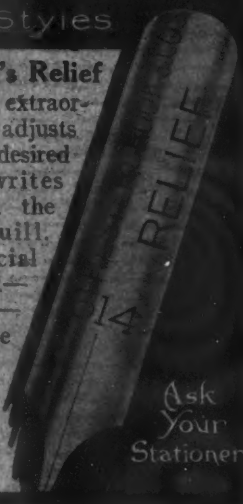

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